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RELATION OF MEGASPORES TO EMBRYO SACS IN ANGIOSPERMS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 110

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The recorded cases of unusual conditions in the angiosperm embryo sac are multiplying. Especially is this true in reference to the occurrence of more than eight nuclei in the ante-fertilization development of the gametophyte. There is a tendency to regard the latter cases as representing a more primitive condition of the gametophyte, and to exclude from consideration a general view of the genesis of the nuclei. It seems to be a fitting time to call attention to certain facts that may interpret this situation, may connect it with other "irregularities," may check the tendency to ill-considered generalization, and may indicate certain things that must be included in any investigation of the embryo sac.

In the genesis of the ordinary angiosperm embryo sac from the megaspore mother cell five successive nuclear divisions are involved, the first two being the reduction divisions (usually resulting in four megaspores with walls), and the other three resulting in the production of eight nuclei from the nucleus of one of the megaspores. The functions of these eight nuclei of the female gametophyte do not enter into the present discussion. Attention is called to the following facts: this genesis begins with the division of the mother cell; the essential part of the process is found in the first two divisions, which cannot be omitted, so far as we know, when fertilization is to occur; the result of these first two divisions is the organization of megaspore nuclei, definitely recognized by their cytological history and structure.

The most familiar illustration of departure from this ordinary sequence is the case of Lilium and its allies. In current description

the mother cell of Lilium is said to "function directly as a megaspore," and the resulting eight-nucleate sac seems to be quite normal. The inference is that the formation of megaspores has been omitted, and that the nucleus of the mother cell holds the same relation to the eight nuclei of the embryo sac that the megaspore nucleus does in ordinary cases. Analysis of the situation, however, shows that this is not true, for megaspores, at least their nuclei, cannot be omitted. The first two divisions from the mother cell are reduction divisions, and therefore the first four nuclei of the embryo sac of Lilium are megaspore nuclei, to be recognized as such by their cytological history and structure. This means that the nuclei of four megaspores have entered into the structure of the female gametophyte of Lilium; and that to complete its ante-fertilization development each of these nuclei divides once. Therefore, in the case of Lilium, there is only one division after the reduction divisions, instead of the usual three; and the total number of divisions is reduced from the customary five to three. In this case the history of an embryo sac containing the usual structures shows a very unusual reduction in the number of successive divisions, and this reduction seems to have been attained by many more monocotyledons than dicotyledons.

The case of Cypripedium[1] is an illustration of a similar reduction; but with the old methods of interpretation it would stand as remarkably different from Lilium and most angiosperms, for the completed embryo sac, ready for fertilization, contains only four nuclei. But in this case the mother cell divides, and one of the daughter cells forms the embryo sac. The first division of the nucleus of this daughter cell is the second reduction division, resulting in two megaspore nuclei. It is these two megaspore nuclei that are involved in the development of the female gametophyte, each dividing once as in the case of Lilium. Therefore, in Cypripedium also the usual five successive divisions are reduced to three; the only difference being that in Lilium four megaspore nuclei are involved, while in Cypripedium only two are used. In her paper Miss PACE calls attention to this comparison, and also to the fact that the elimination of one more division would result in an oogenesis similar to that of animals.

[1] PACE, LULU, Fertilization in Cypripedium. BOT. GAZETTE 44:353–374. *pls. 24–27.* 1907.

In the older papers many records of "three megaspores," "two megaspores," and "no megaspores" appear, which either must be due to incomplete investigation or represent such an elimination of divisions as is shown by Lilium and Cypripedium.

What has been regarded as the most striking exception to the usual structure of the angiosperm embryo sac is the case of *Peperomia pellucida*, described by CAMPBELL[2] and JOHNSON.[3] In this sac sixteen nuclei appear before fertilization; that is, there appears to be one more division than usual. Lately JOHNSON[4] has described a similar condition in the Jamaican *Peperomia hispidula*, in which there are also eight-nucleate sacs.

Fortunately, in the case of Peperomia we know that the mother cell does not divide to form walled megaspores, so that the probable interpretation of the situation is evident. Four megaspore nuclei are formed, all of which are probably involved in forming the female gametophyte. By two successive divisions each of these gives rise to four nuclei, and the result is sixteen nuclei. It follows that the ordinary number of successive divisions has been reduced from five to four; and that if Peperomia had suffered no reduction, there would have been thirty-two nuclei in the embryo sac. In number of divisions, therefore, Peperomia lies between the ordinary angiosperms on the one side, and Lilium and Cypripedium on the other. This condition should be regarded as advanced in the direction of the elimination of divisions, rather than primitive. If an embryo sac derived from a single megaspore should contain sixteen nuclei, it could be regarded as relatively primitive; but the sac of Peperomia could contain thirty-two nuclei and only be normal. *Peperomia hispidula* is interesting in developing eight-nucleate sacs in addition to the sixteen-nucleate ones, which perhaps puts it upon a level of reduction with Lilium. It may have some bearing on the situation to note also that JOHNSON in his account of this species described the first four nuclei of the sac as "arranged in a perfect tetrad," which would be quite natural for

[2] CAMPBELL, DOUGLAS H., Die Entwicklung des Embryosackes von *Peperomia pellucida* Kunth. Ber. Deutsch. Bot. Gesells. **17**:452–456. *pl. 31*. 1899.

[3] JOHNSON, D. S., On the endosperm and embryo of *Peperomia pellucida*. BOT. GAZETTE **30**:1–11. *pls. 28, 29*. 1900.

[4] JOHNSON, D. S., A new type of embryo sac in Peperomia. Preliminary notice. Johns Hopkins Univ. Circ. **1907**:19–21. *pls. 5, 6*.

megaspores. In fact, it may not be out of place to state that JOHNSON has expressed the opinion privately that these four nuclei are those of megaspores.

Recently CAMPBELL[5] has examined *Pandanus odoratissimus* and *P. Artocarpus*, and found usually fourteen nuclei in the embryo sac. At the four-nucleate stage there is the usual arrangement of two micropylar and two antipodal nuclei; but the former do not divide, and the latter give rise to twelve nuclei. If this record is confirmed by tracing the history of the nuclei, there is introduced in this case an irregularity in the succession of divisions. It may be assumed, subject to subsequent observation, that four megaspore nuclei are involved in the formation of these fourteen nuclei; and the irregularity would consist in the fact that two of them do not divide; that one of the others added two successive divisions (the elimination of one division); and that the remaining one added three successive divisions (the usual number). There is thus no greater number of divisions than usual, and even a certain amount of elimination. It is interesting to note that if the two micropylar nuclei do not divide and are really megaspore nuclei, the egg is removed from the mother cell by only two divisions, which is the condition of the animal egg. A careful cytological investigation of these divisions would seem to be most desirable.

The introduction of a certain amount of irregularity in the succession of divisions is suggested by the records of several species. For example, in Gunnera,[6] while eight nuclei are common, any number up to sixteen may be found; and in *Trillium grandiflorum*[7] ten sometimes occur. In neither of these species, however, do we have any information as to the behavior of the mother cell in forming megaspores.

In *Ulmus americana*[8] we know that the "mother cell functions

[5] CAMPBELL, DOUGLAS H., The embryo sac of Pandanus. Preliminary note. Annals of Botany **22**:330. 1908.

[6] SCHNEGG, H., Beiträge zur Kenntniss der Gattung Gunnera. Flora **90**:161–208. *figs. 28*. 1902.

[7] ERNST, A., Chromosomereduction, Entwicklung des Embryosackes, und Befruchtung bei *Paris quadrifolia* L. und *Trillium grandiflorum* Salisb. Flora **91**: 1–46. *pls. 1–6*. 1902.

[8] SHATTUCK, CHARLES H., A morphological study of *Ulmus americana*. BOT. GAZETTE **40**:209–223. *pls. 7–9*. 1905.

directly as the megaspore," as in Peperomia, and in the majority of embryo sacs there are eight nuclei (the normal number of nuclei, but an elimination of two divisions); but sometimes there are "twelve or more nuclei" (meaning another division, but still one less than the usual number).

The situation among the Araceae deserves attention, for great irregularities in the embryo sac have been observed.[9] In Aglaonema the nuclei are four to twelve; while in Nephthytis they are reported as ranging in number from two to twelve or thirteen. Unfortunately, in these cases we are not sure of the behavior of the mother cell; but so far as the records for Araceae go, the mother cell divides once or not at all. It is needless to draw any conclusions as to the amount of reduction involved in the four nuclei of Aglaonema or the two nuclei of Nephthytis until we know something of their history. At all events, there is a reduction of the ordinary number of divisions in these forms; and this is probably true even in the cases where twelve or thirteen nuclei appear.

The only case reported, in which there remains some evidence that an additional free nuclear division may occur, is that of the Penaeaceae, a small African group of shrubby xerophytes restricted to southwestern Cape Colony. In a preliminary note, STEPHENS[10] has announced his results with five species, representing three genera (Sarcocolla, Penaea, and Brachysiphon), and his account applies to all of them. There are sixteen free nuclei formed in the sac before fertilization, which are said to be derived from the innermost one of a row of three megaspores. In such a case three "megaspores" are as good as four, except that the outermost cell is not a megaspore. The testimony breaks down, however, at the critical stage, for the investigator is not certain as to the "row of three." Of course if it should turn out to be a "row of two," the megaspore condition would be that of Cypripedium, followed by the usual number of divisions. The behavior of the nuclei, however, suggests strongly

[9] CAMPBELL, DOUGLAS H., Studies on the Araceae. The embryo sac and embryo of Aglaonema and Spathicarpa. Annals of Botany **17**:665–687. *pls. 30–32.* 1903.
———Studies in the Araceae. III. Annals of Botany **19**:329–349. *pls. 14–17.* 1905.

[10] STEPHENS, E. L., A preliminary note on the embryo sac of certain Penaeaceae. Annals of Botany **22**:329, 330. 1908.

that four megaspore nuclei are concerned, and that there is no "row" developed by the mother cell at all. It is a very interesting performance as described; for the original nucleus of the sac produces four nuclei in tetrahedral arrangement; these four separate and become parietally placed (one micropylar, one antipodal, two equatorial); each of the four produces a group of four nuclei; three nuclei of each group organize after the fashion of an egg apparatus; and the four free nuclei pass to the center of the sac and fuse to form the primary endosperm nucleus. We have here at least the assurance of simultaneous successive divisions, which we do not have in the case of all 16-nucleate sacs. If four megaspore nuclei are involved in this organization, the reduction in the number of successive divisions is just that which probably occurs in Peperomia.

Some evident conclusions may be drawn from the above statement, and they should be of use in investigations of the angiosperm embryo sac. The nuclear divisions within the embryo sac vary in character; they may include both reduction divisions, the second one, or neither of them (the usual case). The appearance of more than eight nuclei in an embryo sac is no evidence that there has been any more than the usual number of successive divisions. As many as thirty-two nuclei may appear in an embryo sac without increasing the usual number of divisions. It is absolutely necessary to trace the nuclear succession from mother cell to completed embryo sac before any safe conclusions can be drawn as to the significance of the conditions observed within the sac. The cases of an increased number of nuclei, as in Peperomia, which have sometimes been cited as showing a primitive condition of the sac, have actually turned out to be cases of reduction from the ordinary condition. There is a tendency among many groups to eliminate the divisions that follow the two reduction divisions, but the tendency is not general among angiosperms, since among the Sympetalae it does not seem to exist; hence the forms which exhibit it may be regarded as more or less specialized in this feature.

If an angiosperm embryo sac should be found containing sixteen or more nuclei derived from a single megaspore nucleus, it may be regarded as relatively primitive; but such a sac has not yet been demonstrated.

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THE PHYSIOLOGY AND DEVELOPMENT OF SOME ANTHRACNOSES[1]

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(WITH SEVENTEEN FIGURES AND PLATE XI)

The group of fungi commonly known as the anthracnoses, including the genera Gloeosporium and Colletotrichum, has received much attention from botanists during the past few years. It has been worked from the economic and scientific standpoints, the former being a very important aspect. Many of our most important diseases of orchard, farm, and garden crops are due to some member of these genera, the annual loss to the country reaching into millions of dollars. The bitter rot fungus alone in 1900 cost the apple growers of this country $10,000,000 or more (**46**). The bean anthracnose, due to *Colletotrichum lindemuthianum*, sometimes causes almost a total loss of the bean crop, and other members of the group cause losses in proportion. In some sections certain crops have ceased to be raised on account of the ravages of these fungi.

From the scientific standpoint the group is interesting on account of the peculiar polymorphic life-history of the different members. Until fifteen or twenty years ago, the anthracnoses were known only in the conidial stage. Previous workers were mostly systematists who did little more than describe in a few lines the conidial fructifications; but about fifteen years ago the perfect stage of one of the species was found, and this gave an impetus to the study of the group. Since then the perfect stage of several species has been found.

The history of previous work is familiar to most mycologists through recent papers, and references to this will only be made in connection with the discussion of the different forms.

Some would limit the use of the word anthracnose to those fungi having an ascigeral stage, as in the genus Glomerella; but I prefer to use it, as commonly used, for all fungi having a Gloeosporium-like conidial stage.

[1] Contribution from the Department of Botany, Cornell University, No. 125.

I have had three points in view in studying this group: (1) To work out the perfect stage of as many forms as possible and to make a careful study of it. All the perfect stages of Glomerella that have been found are very similar, and some writers have gone so far as to say that there is only one species. There also seems to be a difference of opinion as to the structure of the perfect stage. Glomerella was described as aparaphysate, but recently SHELDON (**39**) has reported the presence of paraphyses. Several forms have been studied to obtain some evidence on this point. (2) To determine if the forms of Gloeosporium found on apple represent a single species or more than one. The true bitter rot fungus occurring on apples in the south spreads rapidly and causes a great deal of damage, while the form occasionally met with in the north spreads slowly and causes but little damage. The form from the south produces perithecia in abundance on various culture media; the northern form was studied carefully by Miss STONEMAN, but no perithecia were found. CLINTON expressed surprise that she was unable to find them. (3) Can species of Gloeosporium be distinguished by culture methods? Miss STONEMAN has attempted to find characters in this way that would help to differentiate them. It is impossible to distinguish all the species by the characters found on the hosts. The spores in many of them are alike, the acervuli vary but little, and the cross-inoculation experiments that have been tried by various authors have proved but little.

The following paper is based on work carried on with anthracnoses from about thirty different hosts and from fifty or more sources. The forms have been studied in the usual manner. They have been obtained in pure cultures and studied in various artificial media as well as upon the host. The structure of the acervuli, and of the perithecia where found, has also been studied in thin, carefully stained microtome sections. Most of the material was fixed in Gilson's fixing solution.[2] As is well known, the spores of Gloeosporium are imbedded in a gelatinous substance which is very soluble in water. If pieces of the material are put in an aqueous fixative, as Flemming's or chrom-acetic, the spores are almost entirely washed away. The gelatinous

[2] Gilson's fixing solution: 95 per cent. alcohol 42cc, water 60cc, glacial acetic acid 18cc, nitric acid (conc.) 2cc, corrosive sublimate (sat. sol.) 11cc. The material is left in the fixer 6–24 hours and washed directly in 70 per cent. alcohol.

substance is not soluble in Gilson's fixer and hence the spores are held in place (see *fig.* 7). While this fixer has not proved very good for nuclear phenomena, it has been very satisfactory for the results desired in this work.

The culture media that have been most used are bean agar, made from an infusion of fresh bean pods; potato agar with 10 per cent. of glucose added; Elfving's nutrient solution (a synthetic medium); and bean pods in tubes. Various other media have been used to some extent, as beef extract gelatin, potato agar plus various organic and mineral substances, sterilized cornmeal, cassava plugs, etc., but these seem to have little value. Some writers have been advising the use of cornmeal for obtaining perithecial stages, but I have had no better results with that than with various other media. Bean agar has proved as satisfactory as any used, several of the forms producing perithecia on it, although not all of them.

Characters of the group

The anthracnoses are recognized by the characters of the conidial stage. The genera mentioned above are very similar; in all the spores are borne in the same way in the same sort of pustule. Colletotrichum is supposed to be separated from Gloeosporium by the presence of setae in the conidial pustule, but as this distinction is a poor one, in the following discussion the name Gloeosporium will be used for all species, except perhaps occasionally where another name is the one in common use.

The spores are borne in pustules underneath the cuticle, the epidermis, or in a few cases underneath several layers of cells. The spore-bearing stroma appears first as a weft of thickly woven mycelium, which increases in size and finally breaks the tissue above, bearing spores in abundance on short conidiophores. The spores are two to several times as long as broad, straight or fusoid, and hyaline. There seems to be some confusion in the literature as to the color of the spores. For some time it went without question that they were hyaline, but in 1894 ALWOOD (1) described the spores of the bitter rot fungus as slightly greenish. Later SPAULDING and VON SCHRENK (33) detected the same color, and since then other writers have almost invariably seen the same tint. SPAULDING and VON SCHRENK say:

"When highly magnified they have a very delicate light green color. This color is quite distinct, and it seems strange that of many observers ALWOOD (1894) seems to be the only one to recognize this greenish color." Looked at with the microscopes commonly used, corrected for two colors alone, the spores do have a greenish tint. Spores were examined with all the different types of microscopes in the Cornell University laboratory, and with one exception, the Zeiss apochromatic lenses, they showed a greenish tint; but with these lenses, which are corrected for three colors, the spores are absolutely hyaline; so we must return to the original conception of the color.

The spores as a rule have one nucleus, though I have occasionally seen two in very large spores. The nucleus appears as a rather large clear area near the center of the spore and generally close to one wall. It is generally clearly seen, though in old spores, or in those beginning to germinate, or in poorly developed spores, it is sometimes not visible. This structure has been noticed by nearly every investigator, but so far as I have found, it has not been recognized as a nucleus. It is spoken of as a "clear hyaline area," a "round spot not granular as the rest," a "vacuole," etc. Studied in stained sections, however, its true character appears. It takes the nuclear stains readily, though it is difficult to distinguish the structure. In some of the related forms, as *Myxosporium corticolum*,[3] large oil drops are sometimes present in the spores, which may be confused with the nucleus, but the latter is distinguished by its lighter color. Oil drops are highly refractive, presenting a slightly greenish tint with the ordinary microscope, while the nuclei do not show it. The nucleus in the conidium is considerably larger than the one directly below in the conidiophore.

As yet the perfect stage of many of the anthracnoses is unknown, but the ascospore form of several has been found recently. In some it has been found several times; but in others it has been found one, two, or at least only a few times. This may be due to the fact that the ascospore forms are rarely developed, or that the investigators have overlooked them, perhaps on account of their rarity or inconspicuous nature.

While the conidial stage of all the forms is very similar, yet even in the few forms worked out they are connected with at least three

[3] *Myxosporium corticolum* Edgerton. Ann. Mycol. **6**: 48–52. 1908.

genera of ascomycetes. According to our present classification of ascomycetes, no two of these genera are in the same family, while some are in widely separated orders. The genera that are at present known to be connected with the Gloeosporium-like conidial stage are Gnomonia, Glomerella, and Pseudopeziza. In the following pages, these different types will be taken up separately.

Gnomonia type

KLEBAHN (**25**) seems to have been the first to connect a Gloeosporium with Gnomonia. As a result of his work on the sycamore anthracnose, extending over several years, he gave a most interesting discussion of the peculiar polymorphism of the fungus commonly known as *Gloeosporium nervisequum*. He studied the fungus both in the field and in the laboratory on artificial media, finding the perfect stage in the late winter and early spring on old diseased leaves that had lain under the trees over winter. Later he was able to obtain it in abundance by cutting out the anthracnosed spots on the leaves and putting them out in wire netting to winter. According to him, the perfect stage begins to develop in the fall and is mature about Christmas or a little later. By careful examination of his material and by comparison with other herbarium material, he was able to identify it with *Laestadia veneta* Sacc. & Speg., which he showed to be a species of Gnomonia, and named it *Gnomonia veneta* (Sacc. & Speg.) Klebahn.

KLEBAHN was also able to show that the conidial stage is polymorphic. While the conidia are in nearly all cases very similar, the manner in which they are borne is different. The types that he found are as follows:

1. The conidia may be borne in acervuli under the cuticle on short basidia. This is the common stage and has long been known as *Gloeosporium nervisequum* (Fuckel) Sacc.

2. The conidia may be borne in acervuli under the epidermis on long basidia. This stage has been known as *Gloeosporium platani* (Mont.) Oud. Before KLEBAHN, both LECLERC DU SABLON (**29**) and J. BEAUVERIE (**5**) had shown that this was but a form of *G. nervisequum*.

3. The conidia may be borne on twigs in pustules, being known

as *Myxosporium valsoideum* (Sacc.) All. and *Discula platani* (Peck) Sacc. VON TAVEL (**44**) previously had connected *D. platani* with *G. nervisequum*, and BEAUVERIE (**5**) had shown that both of these names are but synonyms of *G. nervisequum*.

4. The pycnospores may be borne in cleistocarpous pycnidia on old leaves on the ground. This stage had been found before and, as was shown by KLEBAHN, had been named *Sporonema platani* Bäumler and *Fusicoccum veronense* C. Massalongo.

I took up the study of this fungus in order to confirm KLEBAHN'S work and to find whether the perithecia normally develop in this country. In nearly all cases I was able to confirm KLEBAHN'S results completely. In a few cases, however, there seemed to be some discrepancies. These will be brought out in the following discussion of the life-history.

The disease due to this fungus, as it is commonly seen, appears on the veins of the sycamore leaf, killing a strip on each side of the vein; later it often spreads to other parts of the leaf. The diseased portions die and become brown, generally accompanied by a distortion of the leaf. On the under side of the diseased spots, and occasionally on the upper side the acervuli develop in abundance, being about 100–300 μ in diameter. The conidia develop in abundance on short conidiophores. In moist weather, or when the leaves are placed in a moist chamber, the spores ooze out in creamy white masses or in white strings. They are usually about 10–14 $\times$ 4–6 μ, hyaline, slightly granular, generally somewhat pointed at one end and more or less rounded at the other.

An examination of the leaves in late summer and autumn shows that the petioles have been attacked also. KLEBAHN does not mention this effect of the disease. Diseased patches may be formed by the fungus growing down the petiole from the leaf blade, or they may be entirely distinct from the leaf blade. Quite often, especially in the autumn, these diseased spots are present at the very base of the petiole, where it is attached to the twig. Whether the fungus passes from the petiole into the twig was not determined, though many leaves were examined; but this seems at least possible. Conidial pustules form in these diseased petioles just as on the leaves. The presence of the disease on the petioles often causes a premature fall of the leaves.

When the leaves fall to the ground, the fungus takes on a saprophytic mode of life, continuing to develop on the dead leaves, spreading much more rapidly on them than it did on the living leaves. It often covers considerable areas, sometimes entirely covering the leaf, and on these areas acervuli and conidia are produced in abundance. KLEBAHN in developing the perfect stage cut out merely the affected areas, in order to save time in looking over the leaves in the spring. He does not speak of the saprophytic growth of the fungus on the dead leaf, and perhaps, did not observe it; otherwise he would not have taken the trouble to cut out the spots. The conidia develop in these pustules throughout the winter; they were examined often and each time spores were found that were viable, and they were particularly abundant after a fairly warm period of a day or two. The pustules on the dead leaves do not seem to differ from those developed normally on the leaves in the summer.

During February or March, a different sort of conidial fruit body begins to form in favored positions. In places where the leaves were kept moist, where they were piled up and sheltered from drying, or where they were placed close together between pieces of wire netting, a sort of pycnidium was formed. This is what KLEBAHN (*l. c.*, p. 548) described as the Sporonema or Fusicoccum stage on dead leaves. The conidia are the same in shape and size as those in the acervuli, but the stroma bearing them has been favored by the moisture and has continued to grow until it has completely surrounded the developing spores. These pycnidia-like bodies (*fig. 3*) are grayish to black, not imbedded in the host tissue, and generally covered by a rather hairy growth of hyphae; they vary in size, some being over 1 mm in diameter. While this structure is a closed one and perhaps would be classed as a pycnidium, it hardly seems to be a true one. It is always more or less irregular and nearly always there are trabeculae consisting of strips or masses of the stroma imbedded with the spores (*fig. 3*). This shows that the spores and the pycnidial wall must have been developing at the same time; while in a true pycnidium, the wall is formed before the spores begin to develop.

An examination of the diseased petioles at this time shows the same formation. The pycnidia are developed in the cankered spots so that they appear to be imbedded in the host tissue. In the petioles the

larger ones were obtained, the pycnidium shown in *fig. 3* being from a cankered petiole. Nearly all the diseased petioles contained the covered pustules in abundance.

In favored situations the perithecia develop also on the dead leaves. KLEBAHN was able to see the little perithecia on the leaves in the fall and found them mature about Christmas. These dates differ considerably from those I observed at Ithaca. Leaves on the ground were examined once or twice a week from autumn until the perithecia were mature; and the first appearance of young perithecia was on January 6. They form on the inside of the leaf and are not visible until they rupture the epidermis. Generally a very small three-cornered or irregular piece of the epidermis, perhaps 1^{mm} in diameter, is slightly raised; and this is the first visible evidence of the perithecium. Perhaps the perithecia may have been developing since early autumn, but they could not be seen. At this time they are nearly globose, about 150–200 μ in diameter, and generally reach nearly from epidermis to epidermis. Usually the leaf bulges out on the lower side of the perithecium, so that it is really thicker than the ordinary leaf. At this time the beak of the perithecium is just beginning to form, and the wall consists of four or five layers of small, black, somewhat elongated, thick-walled cells. The asci have not formed yet, but the ascogenous tissue takes a different stain from the surrounding contents of the perithecium. The perithecium seems to lie free in the leaf, and does not appear to be connected with it by hyphae.

From this time the development is very slow. Although in January the perithecia looked as if they were about ready to develop asci and spores, mature spores were found first on April 21, and they were on leaves that were covered and had been kept moist. This difference in the time of maturing the asci as observed by KLEBAHN and myself must be due to the different weather conditions.

While many perithecia were found occurring normally on the fallen undisturbed leaves, the best success was obtained by placing a large number of the anthracnosed leaves in wire netting and putting them in a moist shady place. A large number of leaves packed close together prevented drying out, which seems to be the greatest hindrance to perithecial development. Also keeping the leaves close together

and undisturbed prevents the perithecia from falling out of the leaves. Quite often they grow so large that they push themselves out of the leaf.

The mature perithecium fits exactly KLEBAHN's description of it. It is subglobose or slightly flattened on the upper and lower sides, and is about 150–200 μ in diameter. At the upper side it is elongated into a beak, though this is short compared with other forms of Gnomonia. In most cases it is not more than one-fourth to one-third as long as the perithecium (*fig. 4*).

The asci (*figs. 18, 19*) are long clavate, 48–60×12–15 μ, generally bent at right angles near the base. Near the apex of the ascus the wall is much thickened and the pore is surrounded by a very refractive ring, appearing under the microscope as two white glistening spots, one on each side of the pore. The ascus is eight-spored, the spores (*fig. 20*) being hyaline, 14–19×4–5 μ, straight or slightly arcuate, unevenly two-celled, the upper cell as it is borne in the ascus being several times as long as the lower one.

Still another stage of the fungus is found on the small twigs. When the leaves fall, all the twigs seem to be perfectly healthy, even to the formation of buds. But toward the last of December and until spring, they begin to show the presence of the disease. The diseased portion, which sometimes extends back several inches from the tip, is covered with the Myxosporium stage. The fungus may live in these diseased twigs for more than a year, producing spores when weather conditions are favorable. Most of the twigs remain alive until spring and start to put out leaves; but when the leaves are about one-third grown, they quite suddenly wither and die, presenting the appearance of blight. On badly affected trees a greater part of the leaves die, some large trees being observed which had only a few green tufts remaining.[4] The Myxosporium pustules (*fig. 2*) are scattered

[4] Since this paper was written, papers by VON SCHRENK (Rep. Mo. Bot. Gard. **1907**:81–83) and CLINTON (Rep. Conn. Exp. Sta. **1907**:360. 1908) have come to notice, in which it is claimed that the injury to the sycamore in 1907 was due to frost and not to anthracnose. From an almost daily observation of the trees at Ithaca, I am convinced that frost had practically nothing to do with the injury. The frosts came on May 11 and 21, while the injury developed during the first three weeks in June. Furthermore, the blighted twigs were covered with the perfectly mature Myxosporium pustules, while twigs that were free from the pustules had no blighted leaves.

thickly over the terminal portions of the twigs, forming under the cork layer of the wood and raising it until it is ruptured (*fig. 5*). The

FIGS. 1, 2.—*Gnomonia veneta.* 1, Young trees badly affected with the Myxosporium stage; 2, the same, natural size, shows Myxosporium pustules.

pustules are 500–900 μ in diameter and are entirely filled with the ordinary spores of *Gloeosporium nervisequum.*

This stage is extremely fatal to young sycamore trees. A careful search was made for young trees that could be transplanted for inoculation purposes, but they were found to be very scarce. When some were found, however, the reason for their scarcity was evident; they were being killed by the anthracnose. The young trees had the same appearance as the terminal twigs on the larger trees; the leaves were nearly all killed when they were about one-quarter grown, and the young shoots were covered with Myxosporium pustules (*fig. 1*). The tree on the left in the figure was in the condition of most of the seedlings. Only after careful search was a young tree found that was nearly healthy and could be photographed for comparison; and an examination of the photograph shows that a few leaves are dead on this one. If the time ever comes when this tree is planted for commercial purposes, this disease may develop into a very serious pest in the nursery.

How the fungus enters the twigs was not satisfactorily determined. There are two possibilities; it may pass down the diseased petioles into the twigs, or the twigs may become infected directly from spores. The twigs are infected very close to the apical bud. The presence of the disease on the petioles and the lack of any wounds of any kind on the twigs make it seem possible at least that the former indicates the real method of infection.

Also the question of the fresh infection of the leaves in the spring is not entirely settled. Inoculation experiments tried on leaves in the laboratory were without success. Perhaps the period of incubation is too long to attempt inoculations on branches cut from the tree and kept fresh by standing in water. However, it was useless to attempt inoculations out of doors where nearly every tree was already infected. Several investigators have attempted to infect the leaves artificially, but mostly without success. KLEBAHN after making a large number of inoculations obtained a few successful ones; but one of his checks also took the disease.

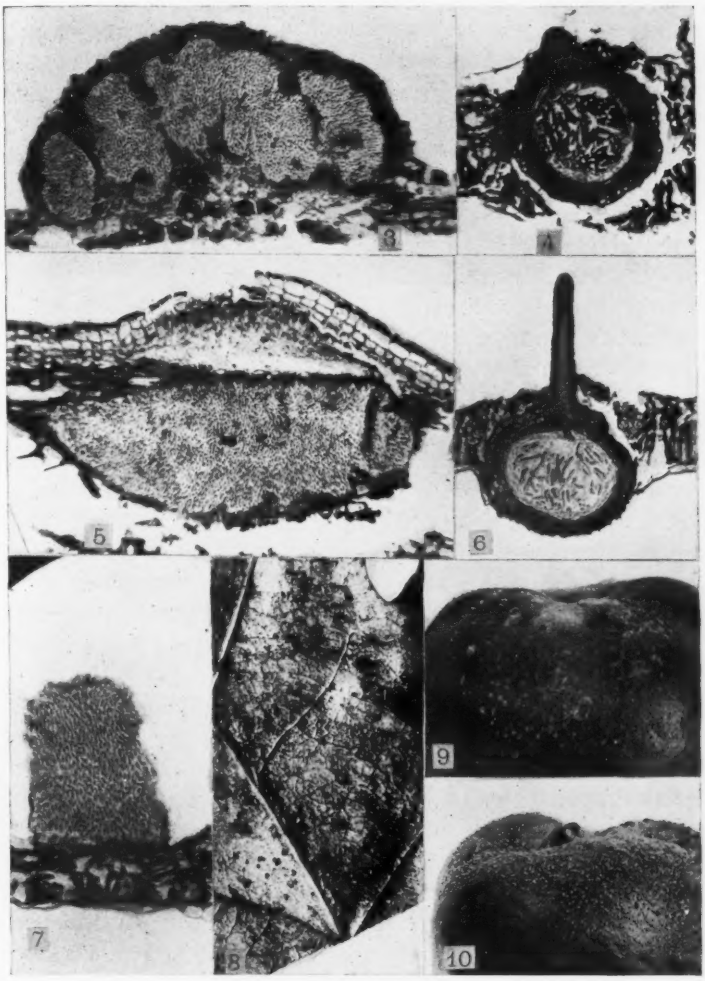
The Myxosporium stage undoubtedly plays the larger part in causing the spring infection of the disease. While the spores, both conidial and ascigeral, are borne in abundance when the leaves are on the ground, they are held together by a mucilaginous substance and are not carried by the wind. The Myxosporium spores on the twigs

may be easily washed by rains to the neighboring leaves and cause infection.

Pure cultures on artificial media were made from all of these different stages and the resulting colonies compared. In all cases the same mycelium and the same colony were produced. The mycelial threads are 1–10 μ in diameter, the small ones being nearly continuous, while the larger ones are closely septate. The colony characters agree perfectly with those given by KLEBAHN. Both conidia and ascospores germinate readily, the latter, however, only from the large cell. The small cell was never seen to send out a germ tube.

This fungus (*Gnomonia veneta*) also occurs on three other hosts at least; *Quercus alba*, *Q. velutina*, and *Q. coccinea*. In 1890 HALSTED (17) described the disease occurring upon white oak as due to *Glocosporium nervisequum*, but there has always seemed to be some question of it. The anthracnose of white oak generally is said to be due to *G. canadense* E. & E. Dead white spots from a few millimeters to a centimeter in diameter are formed, generally scattered over the leaf, though sometimes the tip of the leaf is killed, and sometimes the spots follow down the veins. The conidial pustules and conidia (*fig. 7*) do not differ from those on the sycamore. The two were studied in pure cultures, and the germination and the colony characters seemed to be the same. To make sure, however, that the fungus was the same as the one on sycamore, diseased leaves were put between wire netting and placed out of doors to winter in order to obtain the ascigeral stage. As on the sycamore, the fungus spread over the dead leaf and in late winter produced perithecia in abundance. The characters of perithecia, asci, and spores are the same as in those produced on the sycamore, with the exception of the length of the necks of the perithecia. Outline drawings of the asci and spores are shown in *figs. 21* and *22*, so that they may be compared with those from the sycamore.

The necks of the perithecia on the oak averaged much longer than those on the sycamore, some being as long as the body or even longer. Those on the sycamore have very short necks, or in some cases necks were almost wanting. This single difference does not seem to me to be sufficient to separate the forms as distinct species. The length



FIGS. 3–8.—*Gnomonia veneta.* 3, Sporonema pustule on petiole of fallen sycamore leaf; 4, perithecium in sycamore leaf; 5, Myxosporium stage on sycamore twig; 6, perithecium in *Quercus alba* leaf; 7, acervulus from *Quercus alba* leaf; 8, *Quercus alba* leaf, showing the perithecia, ×2.5.

FIGS. 9, 10.—Apple, inoculated with the Gloeosporium (*Colletotrichum gloeosporioides*); 9, from the orange, showing hairy pustules; 10, from raspberry canes.

of the neck in this genus seems to be quite variable. While KLEBAHN found that the necks of *Gnomonia veneta* from sycamore leaves were very short, on sterilized leaves in the laboratory, on which he also produced the perithecia, the necks were very long. I have also found in my study of *Gnomonia rubi* Rehm., a form found on blackberries, that the same variation occurs. The necks in pure culture were twice as long as those growing normally out of doors. Since this is the only difference observed between the forms on sycamore and white oak, it seems best at present to consider them the same.

The perithecia on the oak leaves also very often push themselves entirely out of the leaf (*fig. 6*). There is often no leaf tissue below the perithecium, but its beak passes entirely through the leaf and projects on the opposite side. The large perithecia are easily seen on the leaf with a hand lens, when they appear as black globose bodies apparently lying on the surface (*fig. 8*).

The spores are unevenly 2-septate, as in the form on sycamore. In germination, the spore swells considerably and then sends out tubes from any place on the wall of the larger cell (*fig. 26*).

The Sporonema stage was not observed on the white oak, though leaves were examined repeatedly for it; but it developed on oak leaves that had been put in tubes, sterilized, and inoculated with a pure culture from the conidial stage on the leaves. The tubes were kept in a cool place during winter to see if the perithecia would develop. On examination in the spring, no perithecia were found, but there were many pycnidia-like pustules, perfectly homologous with those that developed on the sycamore leaves normally.

The Myxosporium stage was found on the ends of twigs on a few trees about July 1, the twigs being killed back in the same manner as the sycamore twigs. However, on the white oak the young leaves did not start to develop and then die, as on the sycamore; but the twigs were killed before the leaves started. Anthracnosed spots on the leaves were numerous in close proximity to the diseased twigs, while they were fewer where no diseased twigs were found. It seems very evident from this that the Myxosporium stage is very instrumental in the early infection of the leaves. The spores in the pustules were not different from those on the leaves, and furthermore, they produced the same colony in agar.

On leaves of *Quercus velutina* also there was found a fungus which does not seem to differ materially from the true *Gloeosporium nervisequum*. The disease, which was very common around Ithaca in the summer of 1906, appeared on the leaves in late summer, dead spots being formed 1–2^{cm} in diameter. The spots were not white, as on the leaves of *Q. alba*, but brown. Sometimes the disease killed a large portion of the leaf, but generally it appeared merely in spots.

The acervuli were scattered on the under-surface of the dead spots. The spores are somewhat larger than those on the sycamore, being about 15–20×6–9 μ. This difference seemed at first to separate it from the form on sycamore; but when the two were grown side by side on plates, the difference was not observable. The spores produced in pure cultures at first seemed to be slightly larger than those from the sycamore, but very soon they became the same size (about 9–14×4–6 μ). Only one difference was noticed between the two forms on artificial media. Both forms on bean pods covered the substratum with a grayish to blackish growth and then grew over the liquid in the bottom of the tubes. On this growth, from the liquid especially, in the culture from *Q. velutina* there oozed out large drops of golden yellow liquid, which were so abundant that they almost covered the surface. As the culture became older, these drops dried to yellow, waxy crusts. On the form from sycamore no such golden drops were produced. In other ways the two forms were indistinguishable on artificial media.

In the spring on a few twigs there was also found the Myxosporium stage. The young twigs were killed before the leaves started, and were killed back 15–20^{cm} from the end. They were covered with pustules similar to those from Platanus and *Q. alba*. A culture made from the spores produced a colony identical with the others.

Diseased leaves of *Q. velutina* were also put out in wire netting to see if the perfect stage would develop. In the spring near the anthracnosed spots were found small scattered perithecia, which were identical with those found on the white oak leaves. The asci and spores are illustrated in *figs. 23* and *24*, so they may be compared with the same from the other hosts. Cultures from the ascospores

again gave the same mycelium and conidia as had been obtained from the imperfect stage.

While there are some slight differences between this form and the one from sycamore in the size of the conidia and effect on culture media, these do not seem to be sufficient to make a new species, especially since the large conidia do not appear on artificial media. Perhaps the slight difference found on culture media was due to the previous growth for some time on different hosts. The one from white oak, after being grown for several months on artificial media, lost some of the characters it originally had. The zonate growth of the colony became less marked, and the aerial tufts containing pustules were more feebly developed. The difference between the forms on *Quercus velutina* and *Platanus occidentalis* was, perhaps, no more marked than the difference between cultures of the same fungus after growing for different periods on artificial media.

Search on other oaks has also resulted in finding the Myxosporium stage on twigs of *Quercus coccinea*. The disease was not different in appearance from that on the other hosts, and a culture of the spores also gave a colony similar to the colonies from other hosts. Anthracnosed leaves of *Q. coccinea* have not been found, but they undoubtedly can be found at the right season.

While no satisfactory inoculation experiments were carried on, it seems almost certain that these three forms are the same. They are at least no more than biological species. Attempts were made to inoculate young oaks in the greenhouse, but they were unsuccessful, even when the conidia were placed on the same species of oak from which they were developed.

Whether *Gnomonia veneta* occurs on any other host is a question; there appears no reason why it should not be found on other oaks. HALSTED (16) has described the disease as occurring on red maple (*Acer rubrum*). While this is very possible, proof of it will only appear when the perfect stage is developed and the forms are compared on culture media. No Gloeosporium has been found on maple near Ithaca since this investigation was begun, so there has been no chance to find the perfect stage. However, if it does occur on maple, it seems strange that it has not been found, as the fungus is so common on the other hosts.

In adopting a name for the sycamore fungus, KLEBAHN used the specific name first given to the perfect stage (*veneta*). Adopting the first name applied to the perfect stage seems to be the general rule among European mycologists. In America, however, there are many who believe that the first name given to any stage should be the one used. If the latter rule is adopted, then the name *veneta* cannot hold. The first name given to any stage was *Fusarium platani* Mont., and hence the fungus would have to be called *Gnomonia platani* (Mont.). This will only be settled, however, when botanists come to some conclusion as to the nomenclature of polymorphic fungi. Also if we wish to be consistent in our use of names of the imperfect stage, we should use *Gloeosporium platani* instead of *G. nervisequum*. However, it is of little importance what the imperfect stage is called, it is at best only a synonym.

The synonymy of this fungus as given by KLEBAHN includes sixteen names. To this may be added the following: *Gloeosporium canadense* E. & E. Jour. Myc. **5**:153; *Myxosporium platanicolum* E. & E. Proc. Acad. Philad. **1894**:572 (distributed in N. Am. Fungi as 3180). The form on *Quercus velutina* does not seem to have been described.

Anyone wishing more of the details of the life-history of this fungus must consult KLEBAHN'S work, where every stage is described in fullest detail.

Pseudopeziza type

The genus Pseudopeziza was first connected with a Gloeosporium by KLEBAHN (**26**) in 1905, who found the perfect stage of *G. ribis*, a form common on currant leaves, to be *P. ribis* Klebahn. He developed the perfect stage by putting the leaves out of doors in a protected place to winter; and in the spring he found it in abundance.

My investigation of this form has been very limited. Only a small amount of material was obtainable and little more was accomplished than to study the form in pure culture. An attempt was made to produce the perfect stage, but it was without success.

Glomerella type

Although a great deal of work has been done on this group of anthracnoses, the results obtained have been less satisfactory than

those obtained from the other types. The great majority of the anthracnoses that have been described belong in this group. Nearly all those of fruits—and a glance at the literature will show that there are scores—and a large percentage of the forms on herbaceous stems seem to belong to this type. The problems concerned and the difficulties that confront the investigator become more evident the longer the group is studied. Little more can be done in this paper than to add to our knowledge of the biology and physiology of the forms studied. This type is sharply separated from the others, not only in the characters of the perfect stage, but also in those of the mycelial and conidial stages. Nearly always one can recognize this type at a glance.

Some of the evident characters are as follows: (1) The spores ooze out of the acervuli in pink masses or strings; so far as has been observed, the spore masses in the Gnomonia and Pseudopeziza types are white, cream-colored, or yellow. This may not be a sure criterion, but it seems to hold in nearly every case. (2) In artificial cultures, especially where nutrition is lacking, and sometimes on the original host, the dark-colored secondary spores or appressoria are developed; in no instance have these been observed in the other types, although they have been carefully searched for. (3) The mycelium in pure culture varies but little in diameter; this separates these forms at least from those of the Gnomonia type. Other minor points that help to place the forms in this group are the rapidity of growth, the presence of small black wefts or crusts of mycelium in the culture medium, and the presence of a dark-greenish pigment in old mycelium, especially on sugar media. The last two characters are not always present, but their frequency makes it advisable to mention them here.

Most of the work that has been done on species of Gloeosporium, especially by American botanists, has been done on this group. The papers of Miss SOUTHWORTH, Miss STONEMAN, CLINTON, SPAULDING and VON SCHRENK, SHELDON, ATKINSON, and SHEAR have dealt principally with these forms.

GENERAL DEVELOPMENT OF THE FORMS

As to the life-history and development of these forms, little needs to be added here. Each goes through the same stages in develop-

ment, and these have been described during the past few years for a number of forms, by a number of investigators. Only a few things which do not seem to have been made clear need to be mentioned.

The conidia germinate very readily in water or in nutrient solution, generally within three or four hours. The germ tube may be sent out from any place on the spore, but in most cases the first tube originates near one end. It rarely comes exactly from the end, but very close to it, so that it appears to extend at an angle to the main axis of the spore (*figs. 30, 36, 37*). If it came exactly from the end, the germ tube and the spore would lie in a straight line. In some cases the tube does appear to come from the end, but this seems to be uncommon as compared with the other method. After the first germ tube, several more may develop apparently from any place on the spore.

Germination differs somewhat in different media. Rarely in nutrient solutions does the spore become septate in germination. In water, however, the germ tube is much smaller and generally the spore becomes septate. This variation in germination in different media seems to be characteristic of all members of this type. It is interesting at this point to note a recent paper by DELACROIX (**12**) on *Gloeosporium musarum*. In studying the germination of its spores, he found that they nearly always became septate. Miss STONEMAN (**43**) some years previously, in working on the same form, had figured the spores as continuous. DELACROIX was undecided whether to call the form he was working with a new species or not, as this was the only point of difference. If he had germinated his spores on different media, he undoubtedly would have found both types of germination.

If germination takes place in a medium lacking nutrient material, as water, the germ tubes grow only a short distance and then form at their tips rather large brown cells more or less variable in shape (*figs. 32, 33*). These have been spoken of variously by different investigators as secondary spores, appressoria (HASSELBRING **24**), etc. They germinate readily under the right conditions, although some seem to have had difficulty in obtaining germination. If nutrition is still lacking after the brown cell germinates, another similar one may be formed at the end of this germ tube (*fig. 32*).

Quite often, however, when a conidium germinates in water, there may be formed at the end of the spore or at the end of a short germ tube a small hyaline conidium perfectly normal except as to size. This was observed by ATKINSON (**3**) from the form on cotton, and by HALSTED (**22**) from a form on *Podophyllum peltatum*, but it does not seem to be peculiar to these forms, for it is rather common in all members of this type.

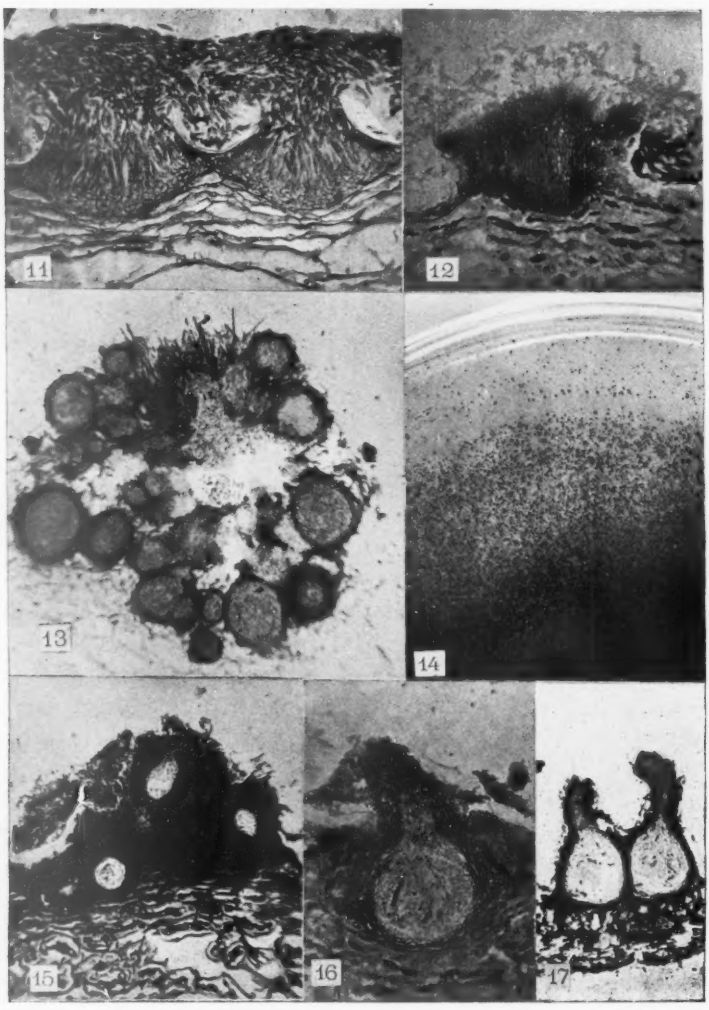
Under proper conditions some forms, either on artificial media or on the original host, develop the perfect stage abundantly. During the past few years this stage has been found from a number of different hosts: from privet, orchid, pepper, red raspberry, and vanilla (?) by Miss STONEMAN (**43**); from Dracaena (**38, 39**) and guava (**37**) by SHELDON; from apple by CLINTON (**10**); from grape, cranberry, Ginkgo, cotton, rubber plant, honey locust, and bean by SHEAR and WOOD (**40**); from Artocarpus by DELACROIX (**13**); from Cattleya by MAUBLANC and LASNIER (**27**), described as a Physalospora. Several other forms described as Physalospora, Laestadia, and Phomatospora undoubtedly should be placed here. During the past two years I have worked with the ascigeral stage from the following hosts: apples from Missouri and Illinois; Dracaena from West Virginia; rubber plant from West Virginia; cotton from Georgia; *Coelogyne cristata, Sarracenia purpurea, Coffea arabica*, and *Anthurium warocqueanum* from the Cornell University conservatory; quince from an orchard in Ithaca, N. Y.; and *Asclepias syriaca* from Ithaca. The last named has been known in the conidial stage as *Gloeosporium fusarioides* E. & K. This is the first time that the perfect stage has been reported from the last five hosts. The perithecia, asci, and spores are very much alike from the different hosts. The following description, based on the perfect stage as it appears on the apple, would fit in nearly all cases the other forms as well.

On apples from the south-central states affected with the bitter rot, the perfect stage seems to develop readily. Apples were received from Illinois and Missouri, and in both cases perithecia were found on the surface accompanying the acervuli. There seems to be considerable variation in the manner in which the perithecia are borne on the apple; *figs. 15* and *16* illustrate perhaps the extremes, the latter having been made from perithecia on apples from southern Illinois.

The perithecia from the Illinois collection were single or collected in twos or threes partially or nearly imbedded in the tissue of the host, and the necks were surrounded by a thin layer of pseudo-parenchymatous fungus tissue. They were generally about 70–125×175–225 μ, the necks being sometimes 50–60 μ in length. The perithecial wall was composed of three or four layers of narrow, long, black, thick-walled cells. Sometimes two perithecia fused, so that there was one internal cavity with two ostioles. At the base of the perithecia there were generally large, dark-colored hyphae made up of nearly globose cells 6–8 μ in diameter (these show plainly in the photomicrograph). *Fig. 15* was made from apples received from Missouri. The perithecia here were not imbedded in the host tissue, but were at the base of the conidial stroma; and the perithecial wall gradually blends into the pseudo-parenchymatous fungus tissue. Necks were almost entirely lacking on these perithecia; in other points they were identical with those described above.

The perithecia develop readily on bean agar, the best success having been obtained with that medium. They appear in raised masses or nodules scattered over the surface of the plates. These masses are black, and by the time the asci are mature they may be 2 to 3^{mm} in diameter. The perithecia (*fig. 13*) form around a small stroma of pseudo-parenchymatous tissue, and are quite variable in shape and size, being 80–140 μ thick×120–225 μ long. The apex may be slightly prolonged into a neck or not, though in no case is it very pronounced, and there seems to be no definite direction for the neck; some of them opened directly into the underlying agar. In a plate kept in the incubator at a temperature of 26–30° C., the nodules of perithecia were generally visible in four to six days, and the asci were generally mature in sixteen to twenty-one days.

The asci are 50–80×8–10 μ, clavate, almost entirely filled by the eight spores; the wall is hyaline and sometimes difficult to see except with fresh material. The spores are hyaline, slightly curved, rounded at the ends, granular, and possess a large clear nucleus near the center and on the concave side of the spore. The spores are irregularly biseriate in the ascus, and are very quickly shed after maturity. The asci go to pieces and the spores ooze out of the neck of the perithecia. What causes the spores to leave the perithecium was not determined.



FIGS. 11–17.—*Glomerella type.* 11, acervuli on tomato; 12, acervulus on apple from Missouri; 13, nodule of perithecia of *Glomerella fructigena*, perithecia in plate culture; 14, variation from *G. fructigena*, perithecia scattered, ×2.5; 15, *Glomerella fructigena*, perithecia on apple from Missouri; 16, *Glomerella fructigena*, perithecium on apple from Illinois; 17, *Glomerella cincta*, perithecia on *Coffea arabica* leaf, showing the long perithecial necks.

Sections of perithecia a little past maturity showed the spores held together in a mass just outside and at the apex of the neck. The whole inside of the perithecium seemed to be empty, with the exception of a few scattered threads. It seems probable from the sections, although this was not determined absolutely, that the ascospores are held together by a mucilaginous substance as well as the conidia.

The question of paraphyses is a much discussed one at present. The genus Glomerella was described by SPAULDING and VON SCHRENK as without paraphyses, but quite recently SHELDON (**39**) has reported their presence in a number of forms, especially in the young perithecia. SHEAR (**40**) has taken exception to SHELDON'S observations, finding sterile threads in the perithecia but believing they were entirely outside of the asci, so they would be periphyses and not paraphyses; later (**41**), however, he calls them evanescent paraphyses. The point is an extremely difficult one to decide. Forms from several hosts have been studied to determine this point. In crushing a fresh perithecium, sterile threads can be easily seen; *fig. 42*, drawn from the form on Dracaena, shows them plainly. These threads are very irregular, many of them much longer than the asci, sometimes branched and sometimes septate. They are very highly granular, in fact the granules are the most prominent part, the wall itself being almost invisible. The difficult question is to determine whether they are between the asci or outside of them. Scores of stained sections have been prepared and carefully examined; some slides have looked a little suspicious, yet never have the threads been seen between the asci with certainty. While the threads take the stain poorly, they can be seen, and appear to form a layer around the asci near the base of the perithecium, but in the upper part of the perithecium above the asci they branch out over them. As the asci and spores break loose from the bottom of the perithecium, they can be seen mixed in with threads. They could hardly be considered evanescent paraphyses, because they remain in the perithecia as long or longer than the asci. It seems best, therefore, to regard the genus as aparaphysate.

The perithecial stages from all of the forms, so far as known, seem to be quite similar. The most variable characters are the size of the spores and the length of the neck of the perithecium. The spores

vary in length from 12 to 32 μ; SHEAR and WOOD (**40**) place the extreme length at 24 μ. While most of the spores are under the latter figure, from perithecia from *Sarracenia purpurea* many spores were seen 30 to 32 μ long; but here all the asci were not eight-spored, some containing two spores (*fig. 45*), while four spores were common. Here, as in other forms where this condition exists, the spores in the few-spored asci are larger than in the eight-spored ones. The length of the neck of the perithecium is also quite variable, and as a rule it is generally longer than those previously described on apples. Miss STONEMAN (**43**) shows some of them to be very long, and SHEAR was rarely able to find any so long. An examination of her slides, however, which are still in the Cornell University laboratory, leaves no doubt that the perithecia were as she illustrated them. Furthermore, perithecia with necks just as long (*fig. 17*) have been seen many times. In the forms from rubber plant, Dracaena, Coffea, and Sarracenia, which produced their perithecia on leaves, the long necks were the rule rather than the exception. However, these same forms in pure culture, with the exception of the form from Sarracenia which did not produce perithecia in pure culture, formed perithecia with short necks. The length of the neck seems to be dependent to some extent upon the substratum. However, the depth to which the perithecia are imbedded in the substratum does not seem to be the controlling factor. The perithecia may be nearly or entirely superficial, or may be nearly or entirely imbedded in the substratum; many of those which were entirely superficial had the longest necks (*fig. 17*).

Just what the factors are that cause the development of the perfect stage is unknown. I obtained this stage from the different forms as follows: (1) By placing portions of the diseased host in a moist chamber and leaving it for two to three weeks. If the perithecia did not develop in this time, it was useless to continue the experiment. The following forms produced perithecia in this manner: apple, orchid, *Sarracenia purpurea*, *Coffea arabica*, *Anthurium warocqueanum*, and *Asclepias syriaca*. (2) From inoculations on plates of bean agar from a fresh culture from the host (apple, Dracaena, rubber plant, and *Coffea arabica*). (3) On bean plugs (cotton). (4) On plates of bean agar from a culture that had been kept alive in the laboratory for over a year (quince).

The composition or density of the substratum or the humidity seems to have but little influence in the production of this stage. However, the interesting fact was noted that, with but few exceptions, all the forms known to have perfect stages are southern or greenhouse forms. Almost everything affected with anthracnose when brought from the greenhouse and placed in a moist chamber produced perithecia. Apples from Missouri and southern Illinois produced this stage; but apples, tomatoes, fruit of *Podophyllum peltatum*, and various other fruits and stems found out of doors in New York and brought into the laboratory, produced conidia in abundance but no perithecia. The form from quince from Ithaca, N. Y., did produce perithecia, but only after it had been grown in the laboratory for more than a year. Perithecia were also developed on *Asclepias syriaca* from Ithaca, but this form was found late in the fall, after a long growth through the summer. It may be that a long-continued production of the conidial stage or a long-continued growth at a rather high temperature are factors in perithecial development. However this may be, it is certain that the ability to produce perithecia may be acquired or lost by the fungus. Sub-cultures have been made from single conidia from a culture in which perithecia were produced in abundance. Some of these would produce the perfect stage, while by no treatment known could others be made to produce it. However, as a general rule, it is an easy matter to obtain perithecia in sub-cultures from a culture that has already produced them. To me it appears as if in this group the ability to develop perithecia is one of the characters that may be acquired if conditions are right, one that is inherited for some time but will be lost eventually if the environment is not suitable. When it is known that these forms vary in other ways, as described later, this seems all the more plausible.

CULTURAL CHARACTERS

There has always been great difficulty in determining the species in this type. As a result many species have been determined by the host. Recently botanists have been questioning the validity of the method, especially since the perfect stages of several have been found to be very much alike. At present SHEAR and WOOD (**40**) take the extreme ground that all whose perfect stage has been found repre

sent one species, or at best varieties of one species. They base their belief chiefly on the fact that the perfect stages are not morphologically distinct; but because two forms have similar perfect stages it does not necessarily follow that they are the same species. In higher plants there are many instances of the flowers of different species being very similar, if not identical, yet no one would hesitate to call them distinct; differences in the vegetative stage, as the shape or lobing of the leaves, may be marked and constant and hence sufficient to separate them in distinct species. The sexual stage is the least subject to modification, and we must expect very closely allied species to be very similar in this stage. This must be especially true in forms in which the perfect stage is only occasionally produced, as seems to be the case with Gloeosporium.

Theoretically, if we should grow two forms side by side on the same medium and should watch their development, we ought to be able to tell whether or not they are distinct. If the growth characters were different, if the colonies formed were distinct, or the effect on the medium were not the same, we should doubt the advisability of calling them the same thing. Miss STONEMAN carried several forms through on different media and was able to separate some of the different forms by means of these characters. This method has long been in use in bacteriology for determining species; and recently the method has been advocated by THOM (45) for determining species of Penicillium. He has used it in his work on this genus and has found it satisfactory, claiming that the characters of a species on a standard medium are always the same. No matter how long a species may be grown on some other medium, when it is brought back to the standard medium it immediately returns to its original characters.

A thorough attempt was made to test this method with the different members of the Glomerella type; all of these have not developed the ascigeral stage, but they undoubtedly belong to this type. Cultures from over twenty different hosts were used. Petri dishes, filled with a certain medium, were inoculated at the center with a pure culture. Cultures were made from all the similar forms at the same time, generally three plates of each form. The medium for the set of cultures was made in one batch, so that there was no chance for variation in this factor. Many sets of cultures were made em-

ploying the following media: potato agar, bean agar, potato agar +10 per cent. of glucose, potato agar+malic acid, and Elfving's nutrient solution. A number of sets of these cultures were carried on during the year 1906–7.

VARIABILITY OF FORMS

A most remarkable fact was made evident by the study of the cultures of the various forms. Of the more than thirty collections studied from over twenty hosts, with less than a half-dozen exceptions, all gave at least slightly different characters. Even the two collections on apples from Missouri and Illinois did not give exactly the same characters, but the differences were slight. The two collections from apples in the north, however, gave entirely distinct characters from the more southern forms on the same host. The southern form, especially on sugar medium, was characterized by very rapid growth and a very dark greenish-black color of the substratum and aerial hyphae; while the northern form grew more slowly and had very little dark color. Generally in the latter the aerial hyphae were colored pink from the profuse development of conidia. Even the form on quince collected in New York did not give the same characters as the northern form on apple. The forms on orchid, Coffea, and Sarracenia, collected in the same greenhouse at the same time, were not exactly alike in culture media. They were similar in most respects, but there were slight differences which would appear after many transfers.

What do all of these differences mean? Miss STONEMAN used these in her description of species. THOM declares that in the genus Penicillium all of the forms which show differences are distinct species. However, he found that a Penicillium would always give the same characters on the same medium no matter how long it had been grown on some other medium. A careful study was made of the forms of Gloeosporium to see whether the same species, or rather the same collection, would give the same characters generation after generation. Some of the forms were studied for nearly two years. Instead of the cultural characters coming true each time, a number of interesting variations appeared, some of which are as follows.

A Gloeosporium was collected on apples at Mexico, New York.

At first the colony on sugar media was covered with an erect growth of mycelium which became pink colored with the spores. But after it had been grown for several months on artificial media, the aerial mycelium lost to some extent its erect character, becoming denser and more floccose. Furthermore, the aerial mycelium lost entirely its pink character due to the formation of spores. The same variation also occurred with the collection from tomato. But it is interesting to note that two collections from raspberry stems[5] and another one from apple, which were identical at first with the two forms above, held their characters as long as they were cultivated—in some cases over a year.

The forms from quince and red raspberry, after they had been under culture for some time, underwent slight changes in the color of the agar and the aerial mycelium. In fact, nearly every culture changed its character in time.

An attempt was made to change the characters of a form collected on apples in the north, which had appeared to remain constant, by growing on different media for several months. The following media were used: potato agar, potato agar + 10 per cent. of glucose, potato agar + copper sulfate (1:100,000), potato agar with a drop of lactic acid in each tube, and Elfving's nutrient solution. Transfers were made every ten days to three weeks into fresh tubes of the same medium; so that at the end of the experiment the fungus in each tube had grown for several months, with many generations on the same medium. At the end of three months these cultures were all brought back on plates of potato and glucose agar, and at first the results were striking. For about a week the growth in this medium from the different tubes was quite distinct; however, after two weeks or more these differences gradually disappeared, and the old cultures looked more alike.

After the fungus had been growing for about four months on the different media, it was again brought back to the same potato and glucose agar, and the results were more striking than in the first case. Differences appeared which did not disappear with the age of the

[5] The references to Gloeosporium on raspberry stems under the discussion of this type do not refer to the common raspberry anthracnose, *Gloeosporium venetum*. The latter does not appear to belong to the Glomerella type.

colony. The medium on which the fungus had been growing did not seem to be the cause of the variations, for cultures on the same medium would vary in entirely opposite directions, or cultures from very unlike media would vary in the same way. The characters in which there was considerable variation were as follows: amount of aerial mycelium, some very matted, some entirely strict; color of substratum, from pure white to a dark greenish black; presence or absence of pustules; presence or absence of pink color in the aerial mycelium.

However, the most striking variation that was obtained was with the true bitter rot fungus, the culture being obtained from apples sent from Missouri. The fungus had been grown in the incubator for two or three months, having produced perithecia several times on bean agar, and nothing unusual had been noticed; but very suddenly remarkable variation was seen. A dilution culture was made to obtain single colonies for transplanting, but instead of having one kind of colony in the plate, there were two, and they were very distinct. At first the plate looked as if it had been contaminated, but a study of the two forms showed that it had not. Both forms produced typical bitter rot conidia. Cultures were made of the new form and it was studied carefully with the following results:

On bean agar, for the first day or two, the colony characters were identical with the typical form on apple. At that time the perithecia began to develop, and from that time the differences were remarkable. The typical form produced perithecia in nodules scattered over the media as was mentioned above; but the new form produced them singly, or occasionally in twos or threes scattered over the plate. They were produced in such great abundance that the whole surface of the plate was black with them. They began to form as small tufts of pseudo-parenchymatous tissue on mycelium two to three days old, and developed in such great abundance that all of the nutrient material was used up before they could mature. Mature perithecia were not seen, although they were looked for carefully; it is doubtful whether any of them came to full maturity. The perithecia, however, so far as they could be studied, were identical with the typical form. Conidia formed abundantly, scattered over the surface of the agar, but they

did not form in pustules. On apple it took but slowly, though finally a few small pink pustules of spores were formed. On sterilized bean pods the growth was abundant, in a few days becoming black from the crust of perithecia formed over the surface. But here, as on the bean agar, the perithecia did not seem to develop asci and spores.

Such a large variation may seem incredible, and it may be attributed to a contamination, for which there is always a chance. If this was a contamination and not a variation, either the two forms were present on the original apple and were transferred together unnoticed from the dilution plate to the tube, or the second form must have entered the tube after the transfer was made. As the apples were obtained in the early autumn and this variation did not occur until February, it does not seem possible that the two forms could have been on the apple together. If they had been, they would have been noticed in the cultures, as they were constantly worked with during the fall and winter. The second possibility seems no more likely. The variation came in the middle of the winter, when spores of Gloeosporium would not be liable to be free in the laboratory; and as the new form was totally unlike any of the other species of Gloeosporium in culture in the laboratory, it could not have come from them. The only explanation of the phenomenon is that one or more individuals of the original form changed quite suddenly their course of development under cultural conditions; but whether that is admitted or not, we have at present this new form. It is undoubtedly a Gloeosporium of the Glomerella type, with the development of the perithecia considerably different from other known forms.

Mutations, so far as is known by the writer, have not previously been recorded among fungi, but the form just described seems to be one without question. Whether all of the variations that have appeared in the study of this group should be classed as such is questionable; the minor variations which appeared gradually perhaps should not be so considered. No two individuals of any species are alike, and the variations are perhaps no greater than we could expect among individuals of almost any group. The effect of variation on our ideas of species in this group will be discussed later.

INOCULATION EXPERIMENTS

As is well known, the forms occurring on fruits have been frequently cross-inoculated by different investigators. HALSTED (**20–23**), COBB (**11**), and many others have shown that the forms are easily transferred. HALSTED used fifteen or more fruits and vegetables, and with a few exceptions he was able to transfer the forms at will. This has been repeated by others; and during the past two years I have made many similar transfers. Also the forms on raspberry stems have been grown just as readily on apples as the original culture from apple (*fig. 10*). The forms which HALSTED worked with must have been mostly northern forms.

HALSTED (**20**) also believed that the forms on watermelon and bean were the same, having inoculated both forms on a citron and obtained identical spots. Other workers, as SHELDON (**35**), have failed to get infection by inoculating spores from the melon fungus on the bean; however, the young bean plant is not readily infected from spores from the bean itself.

Little has been done in transferring the forms that are known to produce the perfect stage. Several investigators have transferred the Gloeosporium from the apple to the grape and *vice versa;* and from these experiments it is generally recognized at present that these two forms are the same. Recently SHELDON has also transferred the form from apple to the sweet pea and obtained successful infection; this I have also confirmed. Leaves of young plants in the greenhouse were inoculated from a pure culture from apple; inoculation took readily and dead spots were formed. In one instance the disease followed the petiole back to the stem, and after it had entered the latter the whole plant wilted and died. It is interesting to note that the inoculations of the form found on apples in the north to the sweet pea did not take so readily; only after the plants began to die for want of water did they become infected.

Another experiment was tried with leaves of rubber plant placed in a moist chamber. The forms from Dracaena, *Ficus elastica*, Coffea, and Sarracenia were then inoculated on the leaves. In all cases the fungi took readily, soon producing conidia in abundance; later the forms from Dracaena and Ficus produced perithecia on the leaf.

Inoculations from Dracaena and Coffea to the apple were entirely successful; those from watermelon and bean to the apple were failures. Inoculations from Asclepias to the apple caused infection, but the resulting diseased area looked different from the true bitter rot; no pustules were formed. Inoculations from orange to the apple were successful, but the spot formed was very different from that formed by the bitter rot fungus. The pustules were steel gray, hairy, and raised from the surface (*fig. 9*), and seemed to be identical with the pustules formed by the guava anthracnose on apple, as described by SHELDON (**37**).

While these inoculation experiments are not yet so complete as they should be, they show that we have a number of forms that will grow on different hosts. Whether these different forms occur normally on the different hosts is another question. It is certain also that there are some forms which cannot be transferred to some of the other plants that are normally infected with anthracnose; for example, the bean anthracnose on apple.

ADAPTATION

After one has studied many of these forms for some time and observed the slight difference between them, and after he has watched the variation in single forms, the question of their origin is sure to arise. It is difficult after such a study as the above, where variations take place in a few months, to believe in the fixity of species. Among higher plants some forms are constantly changing, and breeders can now build up a new variety in a few years. If such things are possible in a few generations with higher plants, how much more so must it be with the lower forms, that pass through a generation in a week and may have many generations in a season. These lower forms are excellent organisms with which to study variation, and considerable work of this kind has been done with the bacterial and yeast organisms. HANSEN (**28**) in working with yeasts was able to build up asporogenous varieties by cultivating them under conditions where spore formation was impossible; the varieties became fixed and would not again under any conditions produce spores. He has also been able to build up fixed varieties differing from the parent form in shape of cells and power of fermentation.

Among the bacteria it is a common thing to speak of attenuated forms; that is, forms which have lost some of their characters, due to growth on a different substratum or host from the customary one. Many of the pathogenic forms have been cultivated until varieties have been produced which are unable to produce the poisons characteristic of the parent form.

It is doubtful whether we can say for any form that it is absolutely stable. THOM claims this for the species of Penicillium; and doubtless some forms are more fixed than others. But, as PFEFFER (**28**) suggests, the fact that a form has remained unchanged after growing for two years on a certain medium does not prove that it will not vary in a longer period, or does not prove that it will not vary on some other medium. But the species of Penicillium stand in a different category from those of Gloeosporium. They have been growing for ages as saprophytes on various substances, and have become adapted to a wide range of media, and the forms have become fairly well fixed; but the forms of Gloeosporium are more plastic. Is it not just as possible to have variable forms among the low, fast-growing fungi as among the higher plants? There seems to be no other explanation for the condition that is present in the Glomerella type of anthracnose.

If the forms will vary in culture under constant conditions, should we not expect a greater variation in the open, where the extremes to which the plants are exposed must be many times as great as in the laboratory? In nature, they must at one time or another be subject to every sort of condition under which they will grow. If variation is possible, we should expect to find varieties or forms built up which will come true for at least several generations.

Furthermore, if we admit the fact of variation, we can explain the distribution of forms and also the constant discovery of forms of Gloeosporium on new hosts, or "new species" as they are generally called. Quite often a form is discovered which has never before been found, and immediately it becomes very prominent on account of the great damage it is doing. As a form varies, it may adapt itself to some new host and be able to grow with some vigor. A sudden mutation, like the one described above, might produce a form that would grow immediately on another host; or a form might take but poorly on a new host at first, but after many generations might become

adapted to it. This sudden occurrence of new forms is a vexing question. It may be due to the naturalization of some exotic form, but this does not seem to be satisfactory. The best explanation, at least with variable forms, seems to be the production of new strains or forms from the old ones.

What needs to be done now, and what must be done before we can formulate any idea as to the limits of species among these forms, is to grow them on different hosts and different media for long periods, to see if they will adapt themselves to the new hosts and media and will become fixed. It seems probable from this study that such varieties could be built up, and perhaps sooner than we would expect.

NOMENCLATURE

Some doubt has been expressed lately as to the validity of the genus Glomerella. Some have thought that the forms might very well be put in some of the closely allied genera. There are three other genera which are quite similar, all of which doubtless have had described under them, at one time or another, forms that belong properly to Glomerella. These are Physalospora, Guignardia, and Phomatospora. None of these genera are understood very well by mycologists, and a thorough monograph is needed before we shall be sure of our ground. But there are some characters which seem to prevent the forms of Glomerella from being placed in the other genera. A stroma may be present in the forms of Glomerella, while it is entirely lacking in the others. Other distinguishing characters are the more or less well-developed neck of the perithecium and the lack of definite paraphyses.

The genus Glomerella is extremely variable, and there remains little doubt that some of the individuals would answer very well to the descriptions of the other genera; but it seems that the forms taken as a whole are distinct enough for a separate genus; at least this is the position I should take for the present. MAUBLANC and LASNIER (27) have recently described a perfect stage of a Gloeosporium on an orchid as a Physalospora. Although their material has not been seen, it seems probable that they had but a form of Glomerella. They described their specimen as possessing paraphyses, but their drawings

show a few branched threads entirely outside of the asci; apparently these are the same as are seen in other forms of Glomerella.

The question of specific names is the most difficult one. We have a multitude of closely related forms with a greater number of names. What are we to do with all of these forms? If they were fixed and would vary but little or practically not at all, as seems to be the case with forms of Penicillium, it might be well to call them species, or at least varieties. But when it is difficult to find two collections with the same characters, or to find a form that will not vary on culture media, what is to be done with them? There seems to be little doubt that some of the forms are the same, and that many of the names should be reduced to synonyms; but it also seems that some of the forms are widely enough separated to be considered distinct species. It hardly seems possible that a form that produces large, hairy, steel-gray pustules when grown on apple, as SHELDON (**37**) has described for the guava anthracnose, and as is also the case with at least one form from the orange, could be put in the same species with the one originally found on apple, from which no such a pustule forms.

SHEAR and WOOD (**40**) believe that all the forms whose perfect stage has been found form a single species or at most varieties of one species. They say that all will be considered by them as *Glomerella rufomaculans* or varieties of it. Their use of names, however, is not always consistent. They use *rufomaculans* because it is the first name used for a Gloeosporium on a host of which the perfect stage has been found. Evidently they mean to use the first name applied to any stage. However, in another place in their paper they quote Miss STONEMAN'S species as if she were responsible for the specific name, as, for instance, *Glomerella cingulata* (Stoneman) Sp. & v. Schr. To have been consistent with their use of the name *rufomaculans*, they should have used *Glomerella cingulata* (Atk.) Sp. & v. Schr. ATKINSON (**4**) named the conidial stage and that was the first name. There is great difficulty in getting the right name for these forms. If we use the oldest name applied to the perfect stage, and if we believe, as do SHEAR and WOOD, that all of these forms are the same thing, we must use the name *Glomerella cingulata* (Stoneman) Sp. & v. Schr. But if we follow the other system of using the earliest name applied to any stage, we are in great difficulty. If we follow the latter, we may

use *rufomaculans* until some one develops the perfect stage from some other host, the conidial stage of which was described before *rufomaculans;* and this older name would stand until another earlier one was found. Our names would be in an unstable condition until the perfect stage was developed from the first described Gloeosporium. Furthermore, if we consider the forms from different hosts distinct enough to be species, and also use the name first applied to the perfect stage, the name *Glomerella fructigena* (Clint.) Sacc. must stand for the form from apple.

While the various forms are morphologically very similar, some of them at least seem to be quite well separated from the rest. While the reactions to culture media are not very trustworthy, we can get some idea as to the relationship of the forms. There are some forms which do seem to be very closely related and very likely are the same; the forms from Dracaena, *Ficus elastica*, Anthurium, Coffea, and Sarracenia seem to be very close together and should be considered identical. Whether these are identical with the fungus causing the bitter rot of apples is somewhat questionable, though they are very close to it. There are some differences between them, as, for instance, the size of the germ tube in the germinating conidium, which is much larger in the apple form (*figs. 30, 36, 38, 39*). The forms on Sarracenia and Anthurium seem to be undescribed. The anthracnose, however, has not been found on the Sarracenia plants in the bogs, though it has been looked for. Species of both Gloeosporium and Colletotrichum have been described on the coffee tree. Of course it is impossible to identify the one studied here positively with any of them, but so far as the descriptions go it would fit either.

The form from cotton seems to be quite divergent from the other forms, and doubtless should be considered a distinct species. The cultural characters are quite distinct and it takes but poorly on apple. Also on Elfving's nutrient solution the mycelium breaks up into large cells (*fig. 34*) which are capable of growing into mycelium again, a character which has not been found in other forms. I was not able to bring the perithecia to maturity, that is, the asci did not develop in the perithecia, but SHEAR (**40**) has found a strain which would mature.

The forms from apple have been very perplexing to me. Until

this time it has gone without question that these forms are all the same. SPAULDING and VON SCHRENK (**33**) state that they have seen specimens of the bitter rot on apples in Vermont as late as October. They might have seen apples affected with a Gloeosporium, but it is not certain that the apples were affected with the same form that grows in the south. As was stated above, the two forms on culture media are very distinct, and on the apple itself there is a tendency to divergence. On the apple from the south the conidial pustule as a rule is large, containing much pseudo-parenchymatous tissue which protrudes from the surface (*fig. 12*); while the northern form produces a pustule with little pseudo-parenchymatous tissue, similar to that illustrated from the tomato (*fig. 11*). This distinction does not always separate the two forms, as they often intergrade, but the characters are noticeable in studying the two. Furthermore, the southern form produces perithecia in abundance; while the northern form, so far as is known, never produces them. If we call these two forms the same, we might as well group all of the forms of Gloeosporium into one species and say that Glomerella is monotypic, growing on nearly everything. But if we call them distinct, what shall we name the forms? The names *rufomaculans* and *fructigenum* were given by BERKELEY (**6, 7**) to forms in England on grape and apple. These were found in a latitude comparable to our northern states, and consequently we should think that BERKELEY had a form comparable to our northern one. If this is true, the perfect stage of the true *Gloeosporium rufomaculans* has never been found. This northern form is known to occur on several other hosts, not entirely fruits, besides the apple. The anthracnose of tomatoes has generally been called *Gloeosporium phomoides*, and under this name it has been discussed by several authors. But the culture obtained by me was absolutely identical with the northern form on apple; although the the culture obtained by Miss STONEMAN differed somewhat from her culture from apple. GUEGUEN (**15**) in working on the true *G. phomoides* takes exception to Miss STONEMAN'S conception of the species. It seems that *G. phomoides* is an entirely different thing, and does not belong to the Glomerella type of anthracnoses; hence the name can no longer be used for the anthracnose commonly seen on tomatoes.

The forms from grape stems, raspberry stems, and Podophyllum

fruit are probably only strains of the northern form on apple. At least they will be considered so at present.

While the form from bean has not been studied so much as the others as to its cultural characters, it seems to be distinct. Neither this, nor the form on melons, will grow on acid fruit like the apple. It would have been interesting if SHEAR had given the cultural characters of the form from bean from which he obtained the perfect stage. It should have been compared with the characters of the form from apples in the south. It is possible that the form from apple might develop occasionally on the bean. Even if he did have the true bean anthracnose and it developed a perithecium identical with the apple bitter rot, the habit of growth of the bean anthracnose is sufficiently different to continue calling it a distinct species.

From the evidence available at present, it does not seem advisable to call all these forms the same species. They may finally be placed in one, or at least in a limited number of species, but until the evidence is more certain, it seems best to consider some of them at least distinct. If we use the name first applied to the perfect stage, and we must do this to be consistent with the use of the name *Gnomonia veneta* used earlier in this paper, the names of the perfect stages found by the writer and brought to maturity would be as follows:

GLOMERELLA CINCTA (Stoneman) Sp. & v. Schr., including forms from orchid, *Sarracenia purpurea*, Dracaena, rubber plant, and Anthurium.

GLOMERELLA FRUCTIGENA (Clinton) Sacc. on apple and quince.

GLOMERELLA FUSARIOIDES, n. sp.[6] from *Asclepias syriaca*.

SHELDON (**38**) has recently described the form from Dracaena as a new species, calling it *Physalospora dracaenae*, but from my cultural work it cannot be considered distinct from the form on orchid, the perfect stage of which has already been described by Miss STONEMAN (**43**).

[6] **Glomerella fusarioides,** n. sp. Perithecia nearly free, abundant on the surface of the substratum but more or less scattered, dark brown to black, sub-globose to pyriform, sometimes prolonged into a short beak at the apex, 150–200×140–175 μ. Asci numerous, clavate, 50–75×9–11 μ. Spores irregularly biseriate, straight or slightly curved, 12–18×3–4 μ. Many sterile threads in the perithecium and apparently outside of the asci.

Perfect stage of *Gloeosporium fusarioides* E. & K., which preceded it on the same stems. Stems of *Asclepias syriaca*, October 1907, Ithaca, N. Y.

SUMMARY

In closing the discussion of the Glomerella type, it may be well to summarize briefly the points that have been considered.

1. The Glomerella type is distinctly separated from the other types of anthracnoses by both perfect and imperfect stages.

2. The perfect stage seems to be distinct from nearly related genera of the Pyrenomycetes, is extremely variable, and without true paraphyses.

3. There seems to be a large number of closely related forms, and they are all extremely variable. Furthermore, many forms vary under artificial cultivation and doubtless under natural conditions. While many of the forms may be similar enough to be considered the same, some seem distinct enough to be considered distinct species; at least the evidence is not sufficient to consider them identical.

4. There seem to be two forms on the apple, the forms separated by thermal lines. The form in the southern part of the country differs in the presence of perithecia, a slightly different acervulus, and entirely different cultural characters.

5. From the investigation it seems that too much dependence should not be put on cultural characters for the determination of species. Some of the characters when well marked are useful, but many of the others are too variable.

In closing I wish to express my indebtedness to Professor ATKINSON for aid and criticisms during the progress of the study, and to Professor T. J. BURRILL, Dr. J. L. SHELDON, Dr. H. HASSELBRING, P. H. ROLFS, and Dr. ERNST BESSEY for material for study.

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EXPLANATION OF PLATE XI

Figs. 18–28. Gnomonia veneta

Figs. 18, 19, 20.—Ripe asci, young ascus, and ascospores from sycamore leaf.

Figs. 21, 22, 26.—Asci, ascospores, and germinating ascospores from *Quercus alba* leaves.

Figs. 23, 24, 25.—Asci, ascospores and germinating ascospore from *Quercus velutina* leaves.

Fig. 27.—Conidia from sycamore leaf germinating.

Fig. 28.—Conidia from *Quercus alba* leaf germinating.

Figs. 29–47. Glomerella type of anthracnose

Fig. 29.—*Glomerella fructigena* on apple from Missouri, binucleate conidium.

Fig. 30.—Same, conidia germinating in bean agar.

Fig. 31.—Same, secondary spores formed in old cultures.

Fig. 32.—Same, secondary spores formed by germinating conidia.

FIG. 33.—Gloeosporium from apple from New York, secondary spores formed by germinating conidia.

FIG. 34.—*Colletotrichum gossypium* from cotton; large cells formed in Elfving's nutrient solution; one of these cells germinating, with a young spore at the end of the germ tube.

FIG. 35.—Conidia from quince, germinating in bean agar.

FIG. 36.—Conidia from tomato germinating in bean agar.

FIG. 37.—Conidia from apple from New York, germinating in bean agar.

FIG. 38.—Conidia from *Coffea arabica*, germinating in bean agar.

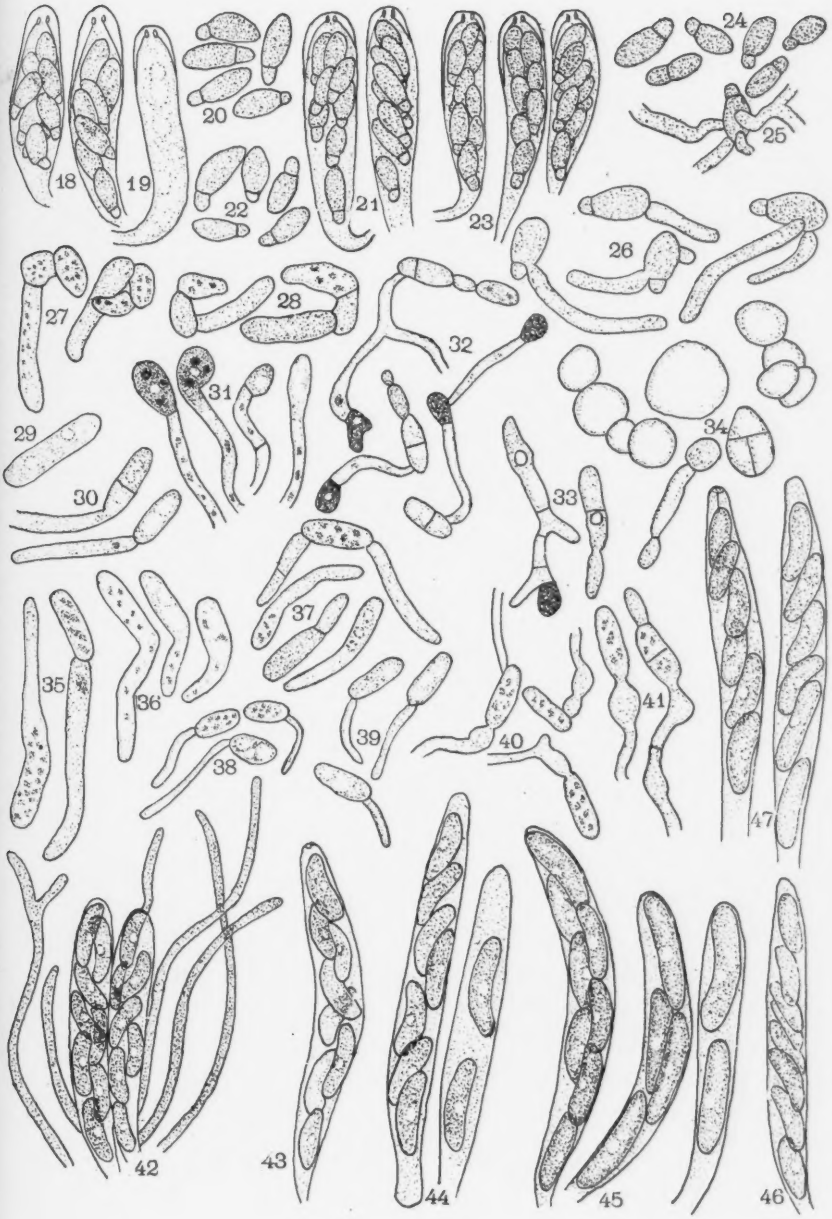
FIG. 39.—Conidia from *Sarracenia purpurea* germinating in bean agar.

FIG. 40.—Same, older stage.

FIG. 41.—Conidia from orchid germinating in bean agar.

FIG. 42, 43.—Asci and periphyses from Dracaena.

FIG. 44–47.—Asci, respectively from leaves of *Ficus elastica*, *Sarracenia purpurea*, quince, *Coffea arabica*.



EDGERTON on ANTHRACNOSES

BRIEFER ARTICLES

ON THE CONTENTS OF THE POLLEN CHAMBER OF A SPECIMEN OF *LAGENOSTOMA OVOIDES*

(WITH TWO FIGURES)

Lagenostoma ovoides is one of the commonest of the ovules occurring in the calcite nodules of the British Coal-measures. It is only specifically distinct from *L. Lomaxi*, which has been attributed by OLIVER and SCOTT[1] to *Lyginodendron Oldhamium*. It appears therefore probable that it belongs to one species of the wide group included under that name, and thus is the ovule of a pteridosperm.

In an oblique section through the micropyle and pollen chamber of a specimen of this ovule, sent me some years ago by Mr. LOMAX, I detected, besides the pollen grains which he recorded, several naked protoplasmic bodies of very characteristic form. One of these bodies is within one of the pollen grains, two are free and entire, and one is cut across. Protruding from three of the grains, which show a considerably ruptured epispore, are bladder-like structures which are clearly surrounded by the endospore. Thus I interpreted the grains as germinating, and (as I mentioned in a paper[2] I was writing at the time) "apparently in the very act of yielding antherozoids like those of Cycas and Ginkgo" (p. 168).

The slide was last year exhibited at the Linnaean Society's rooms, London, on the occasion of the celebration of the bicentenary of the birth of LINNAEUS, and my interpretation having met with general acceptance, I have decided that it should be figured. The many valuable contributions to our knowledge of spermatogenesis (including the recent work on Microcycas by CALDWELL[3]) that have appeared in the BOTANICAL GAZETTE, have induced me to send the account of this remarkable fossil to the same journal.

[1] OLIVER, F. W., and SCOTT, D. H., On the structure of the palaeozoic seed *Lagenostoma Lomaxi*. Phil. Trans. Roy. Soc. London B **197**:193–247. *pls. 4–10*. 1904.

[2] BENSON, MARGARET, *Telangium Scotti*, a new species of Telangium (Calymmatotheca) showing structure. Annals of Botany **18**:161–177. *pl. 11*. 1904.

[3] CALDWELL, OTIS W., *Microcycas calocoma*. BOT. GAZETTE **44**:118–141. *figs. 14*. 1907.

The pollen grains in their enlarged state, owing to germination, measure 70×50 μ.[4] The walls are reticulately thickened and the thinner areolae have in many cases given way and become perforations. The protruding endospore can be seen in two cases to contain cells (*fig. 2, t*), but their nature is difficult to determine. They are probably of the same nature as the cells that can be seen attached to one of the free antherozoids (*fig. 2, t*[1]).

In the absence of any evidence as to their nature, I think it best to suggest that they are possibly of fungal origin, but, on the other hand, they

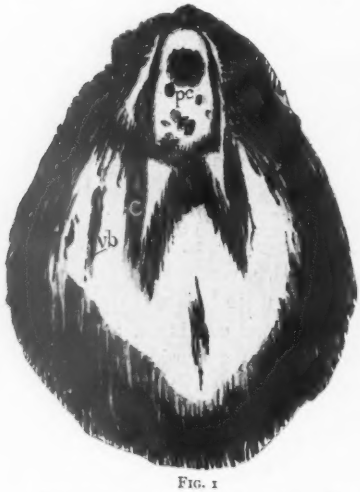


FIG. 1

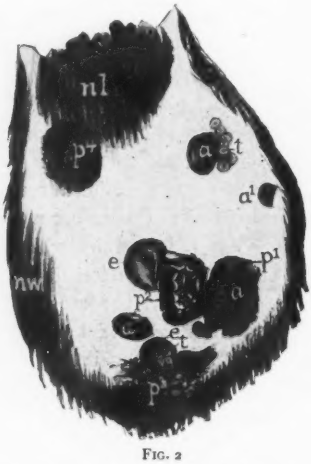


FIG. 2

FIG. 1.—An oblique section through the upper part of the ovule *Lagenostoma ovoides*, ×54; *pc*, pollen chamber; *c*, canopy or inner integument; *vb*, one of the vascular bundles of the integument.

FIG. 2.—The pollen chamber and its contents from the same ovule, ×232; *nl*, tongue of nucellar tissue which supports the pollen chamber; *nw*, nucellar wall of the pollen chamber; *a*, antherozoid; a^1, same cut across; *e*, endospore protrusion; p^1, p^2, p^3, p^4, four pollen grains; *t*, t^1, tissue which is possibly fungal.

Camera drawings from a slide in the R. H. College Collection, C. N. 63. Locality, Dulesgate.

bear a remarkable resemblance to the tissue observed by RENAULT in the pollen grains of Cordaites. If we had a case in which each of these cells gave rise to an antherozoid, it would then be obvious that they were gametophytic. The central body in each cell has the appearance of a nucleus, but is possibly merely the carbonized remains of the whole protoplast.

[4] By an oversight the dimensions were given ten times too small in BENSON, *loc. cit.*

The antherozoids measure 41μ across when free. They are thus about two-thirds the size of those of Microcycas, which appear from CALDWELL'S drawings (*loc. cit.*) to measure 60μ across. Again, they are but one-sixth the size of those of Zamia as figured by WEBBER.[5]

That the antherozoids should be of smaller size than those of recent cycads is explicable when one considers the primitive nature of Lyginodendron and how many fern characteristics it retained. Moreover, there is considerable probability that the number of antherozoids produced by one pollen grain was not limited to two, although there is no evidence as to how many were produced. It is obvious, however, that this pteridosperm did not produce as many as CALDWELL has shown is the case with Microcycas.

Turning now to the figure (*fig. 2*), we see that the pollen chamber is bounded by a thin wall of elongated cells of nucellar origin (*nw*), and that the tongue of nucellar tissue characteristic of the Lagenostoma type of ovule is cut obliquely at *nl*. Within the space thus delimited lie the remains of four pollen grains (p^1, p^2, p^3, p^4). Of these p^1 still contains one antherozoid, and shows but little protrusion of endospore. The grain p^2 is empty; its epispore shows thin areolae, and at *e* the endospore has protruded and shows very faintly one hexagonal cell still preserved near its base. The grain p^3, at the bottom of the exposed part of the pollen chamber, shows clearly five hexagonal cells (*t*), each with a central black spot. The grain has been injured and its contents cannot be determined. Between the grains p^2 and p^3 lies one of the bodies I interpret as antherozoids. The hyaline area of this body appears to correspond with the apex of the coil, but cilia cannot be demonstrated.

A similar body appears on the right near the upper part of the pollen chamber, and this also shows a hyaline area. Accompanying this gamete are the problematical cells which apparently form a continuous tissue and therefore are not chytridiaceous. There are no fungal hyphae connected with them and each cell contains a minute central body. Not far off lies part of a fourth antherozoid (*fig. 2*, a^1), which has evidently been cut across in the process of making the slide.

CONCLUSION

That such bodies as pteridospermous antherozoids should be preserved in the calcite nodules of the Carboniferous rocks will not appear incredible to those who are familiar with the results of palaeobotanical research. In

[5] WEBBER, H. J., Spermatogenesis and fecundation of Zamia. U. S. Dep. Agric., Bur. Pl. Ind., Bull. 2. pp. 100. *pls.* 7. 1901.

the silicified form we have had many records of archegonia from BRONGNIART[6] and RENAULT.[7] The latter devoted considerable time and attention to palaeozoic bacteria, and was the first to record tissue formation in a pollen grain. In calcified material archegonia are found preserved in the megaspores of the Lepidodendreae, and recently SCOTT[8] has recorded the early stages in the germination of fern spores. Still more recently I have had occasion to record a very early stage in the development of the embryo sac in the young megasporangium of Miadesmia.[9] But even with instances such as these, we should not have ventured to identify these antherozoids if it had not been for the antecedent discovery in Ginkgo and the cycads of this type of male gamete. As students of phylogeny, we may well congratulate ourselves that such forms as *Ginkgo biloba* and *Microcycas calocoma* persist to the present time to interpret to us the elaborate pollen chambers of the palaeozoic era. In their turn these paleozoic structures are now giving us some evidence of the great antiquity of the cycad type of male gamete.—MARGARET BENSON, *Royal Holloway College, London University.*

THE EMBRYO OF CERATOZAMIA: A PHYSIOLOGICAL STUDY

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY III

(WITH SEVEN FIGURES)

Ceratozamia is a genus of cycads of the American tropics. Its habit and habitat and the manner in which the ovules are shed shortly after fertilization are described by CHAMBERLAIN (1) in his preliminary note to the study of the reproductive structures.

The embryo has only one cotyledon. This fact was observed by VAN TIEGHEM (2) as early as 1873 in a form which he considered a hybrid between *C. longifolia* and *C. mexicana*, but which was probably pure *C. longifolia*. In 1878 WARMING (3) recorded the monocotyledonous condition of the embryo of *C. mexicana*, adding that the cotyledon arises at one side of the hypocotyl axis and little by little comes to surround it.

Being engaged in an anatomical study of the seedling, the first observation I made was naturally upon this character. In every case in over one

[6] BRONGNIART, A., Recherches sur les graines fossiles silicifies. Paris. 1881.

[7] RENAULT, B., Flore fossile d'Autun. Paris. 1896.

[8] SCOTT, D. H., The occurrence of germinating spores in *Stauropteris Oldhamia*. New Phytol. 5:170–172. 1906.

[9] BENSON, MARGARET, *Miadesmia membranacea*, a new paleozoic lycopod with a seed-like structure. Phil. Trans. Roy. Soc. London B 199:409–425. *pls.* 33–37. 1908.

hundred ovules germinated in 1906, the embryos bore only one cotyledon (*figs. 1, 2, 3*).

When the anatomical study was completed, a preliminary note was received from MATTE (4), who had germinated some seeds provided by CHAMBERLAIN and had begun the study, not knowing that the work was being carried on in this laboratory. MATTE reports that the embryo is monocotyledonous. CHAMBERLAIN (14) in his recent report on Ceratozamia, read before the Chicago meeting of the Botanical Society of America, makes the same statement.

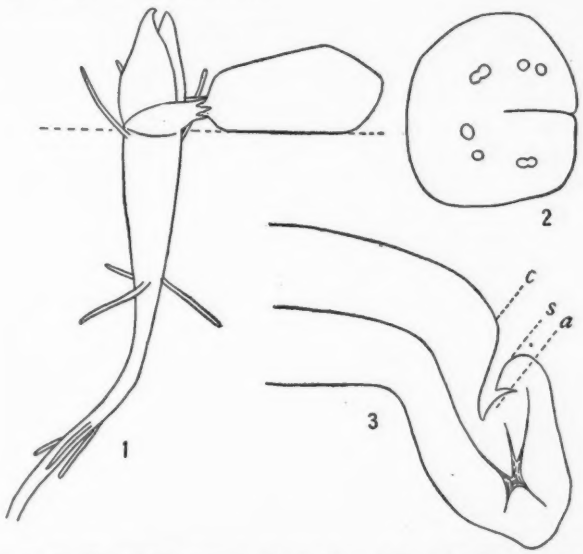


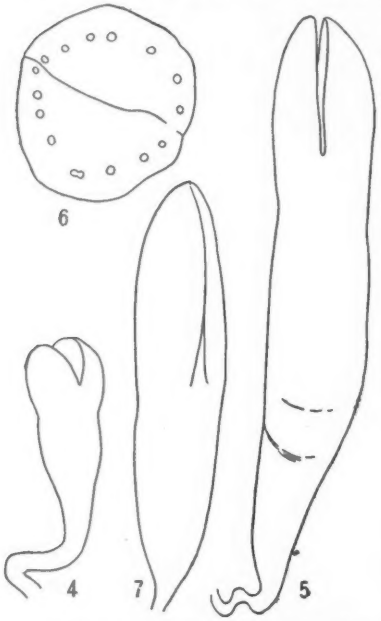
FIG. 1.—Seedling of Ceratozamia showing base of the cotyledonary petiole encircling the stem. Natural size.

FIG. 2.—Cross-section of middle region of cotyledon. ×8.

FIG. 3.—Longitudinal section of seedling in the emergent stage: *c*, cotyledon; *s*, scale; *a*, growing point of stem. ×8.

In other cycad embryos, the cotyledons are often reported as unequal in size. TREUB (5) observed and figured the inequality in *Cycas circinalis*. WORSDELL (6) described a seedling of *Cycas revoluta* in which one cotyledon was considerably shorter than the other. MATTE (7) reports a case in *Dioon edule* in which the vascular strands in the smaller cotyledon are reduced in number, only the rudiments of the missing ones occurring at the base of the cotyledon. He also mentions an inequality in

the size of the cotyledons of *Encephalartos Barteri*. BOWER (**8**) recorded a difference in the size and anatomy of the two cotyledons of *Cycas Seemanni;* and LAND (Chicago) has noted (unpublished) a difference in the size of the cotyledons of *Zamia integrifolia*.



FIGS. 4 and 5.—Embryos developed on clinostat; removed February 3. ×8.

FIG. 6.—Cross-section of middle region of cotyledons of an embryo removed from clinostat February 26. ×8.

FIG. 7.—Embryo taken from soil in green house January 8. ×8.

Outside the cycads one finds the same tendency in seeds of similar habit. SOLMS-LAUBACH (**9**) figured it in an embryo of *Bennettites Gibsoniana*, a fossil relative of the cycads; and COULTER and CHAMBERLAIN (**10**) and LYON (**11**) have recorded it of Ginkgo.

In the course of my anatomical study, I noticed that the cotyledon was a lateral structure and that there was absolutely no external trace of another (*fig. 3*), but certain irregularities in the vascular system made me suspect that the second cotyledon had been suppressed. These irregularities consisted mainly in the suppression of one pole of the root, and the presence of certain rudimentary strands which joined the stem in normal fashion, but whose upper portions ended blindly in the cortex or fused with other bundles. The suspicion was strengthened by the observation that in every case the cotyledon developed on the under side as the seed lay. This latter circumstance led me to think that gravity was responsible for the monocotyledonous condition.

In the following autumn, therefore, fresh ovules were placed in broad pots, covered closely with sphagnum, and placed upon clinostats revolving at different rates of speed. In December the LIVINGSTON porous cup apparatus (**12**) was inserted in order to equalize the soil moisture. At the same time fresh seeds were planted in the greenhouse.

The apparently simple plan of planting the seeds end down was not adopted for two reasons. First, this would not give accurate results, because such a seed as that of Ceratozamia could not be placed and kept in an exactly vertical position, and there is no doubt that a variation from the vertical of only a few degrees is sufficient to bring an organ under the direct influence of gravity. Second, at the time of formation of the growing points, the embryo has been pushed half-way through the massive endosperm in a tortuous and winding path by the elongating suspensor, and it is probable that just at the time when it comes to rest, gravity will determine its position whether the seed be vertical or horizontal.

Rotation on the clinostat seems to have retarded development to a marked degree, but has not otherwise interfered with it. Early in February, the embryos developing on the clinostat were found to have two equal cotyledons (*figs. 4, 5, 6*), while those developing under normal conditions have only one (*fig. 7*). Further, the dicotyledonous embryos have a tetrarch stele in the root and the cotyledonary vascular system is of the usual cycad type.

It can scarcely be doubted that gravity is the main factor in bringing about the inequality reported in the cotyledons of other gymnosperms, and it may be that further experiment will throw some light upon the seeming suppression of root poles. It is possible also that it is to this cause we may attribute not only the monocotyledonous condition long known to exist in some dicotyledons, mentioned by COULTER and CHAMBERLAIN (**13**); but even the condition of certain true monocotyledons whose embryos from their very inception hold a practically unchanged one-sided relation to gravity.

The experimental work is under the direction of Professor CHARLES R. BARNES and Dr. WILLIAM CROCKER.—HELEN A. DORETY, *The University of Chicago.*

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CURRENT LITERATURE

BOOK REVIEWS

North American gymnosperms

Professor PENHALLOW has written a very painstaking and a unique book[1] on gymnosperms. He has taken the North American species (exclusive of cycads), living and fossil, and has constructed a system of classification based upon the anatomy of the mature wood. The original plan had in view the identification of material used for structural purposes; but the investigation soon included the needs of paleobotany, and finally led to suggestions as to phylogeny. The final result includes detailed studies of 92 North American species, 21 Japanese, and 4 Australasian. The enormous mass of detail to be sifted and organized before any satisfactory differential characters based upon wood structure could be made evident can be imagined.

The book is divided into two parts, the first entitled "Anatomy," the second "Systematic." Under anatomy (192 pp.) a detailed account of the regions and elements of mature gymnosperm wood is given, including discussions of durability, decay, and general phylogeny. In the systematic part (157 pp.) a synopsis of the genera and species of Cordaitales, Ginkgoales, and Coniferales is presented, based entirely on wood characters, and including so far as possible the economic values.

Probably the most interesting portion of the book to the general botanist is the chapter devoted to phylogeny. The author has given an excellent illustration of the result of following one set of characters in reaching conclusions as to phylogeny. Morphologists and paleobotanists and anatomists of a different sort have done this before, and with results equally divergent. The morphologists have been checked more frequently than the others, perhaps, for they have been compelled to carry through many different structures that insist upon contradicting one another in reference to any suggested phylogenetic connection. In these latter days, however, morphology, anatomy, and paleobotany are beginning to combine their results in any conclusion as to phylogeny, and the contradictions are multiplying. Professor PENHALLOW has introduced another set of checks, which must either be incorporated in any general conclusions or explained away. He recognizes clearly that his scheme of phylogeny cannot stand, a statement which is true of any scheme based upon one set of characters; but he presents it to be combined with the others in the general result. When different schemes flatly

[1] PENHALLOW, D. P., A manual of the North American gymnosperms, exclusive of the Cycadales but together with certain exotic species. 8vo. pp. viii+374. *pls.* 55. Boston: Ginn & Co. 1907.

contradict one another, it remains to discover the characters that should control, and this becomes a matter of opinion rather than of demonstration.

On the basis of wood anatomy, as interpreted by PENHALLOW, a phylogeny of the gymnosperms is constructed that certainly contradicts many of the conclusions that have been drawn from the other methods of attack. From the Cycadofilices two great divergent lines arise, one being the Cycadophytes, the other the general conifer-like plexus; this view seems reasonable enough. The conifer-like forms are thought to have been derived through such forms as Poroxylon, which in turn forked into Cordaitales and another branch which forked into Ginkgoales and Coniferales. It is interesting to note that the araucarians are made a branch of the Cordaitales stock. The Taxaceae (taxads and podocarps) are made the earliest side branch of the Coniferales stock; then come the Taxodineae, the Cupressineae, and finally the Abietineae, whose most modern and specialized expression is Pinus. Just how this phylogeny can be related to that of Jeffrey, for example, to say nothing of the phylogeny of modern morphology, is not clear. Either mature wood structure is not significant in phylogeny, or there will have to be an extensive revision of our former conclusions.

At all events, it is a good thing to have these facts before us; and the book will certainly be highly useful in its practical applications and also as a great assistance in the recognition of fossil material.—J. M. C.

NOTES FOR STUDENTS

Items of taxonomic interest.—W. N. CLUTE (Fern Bull. **16**: 1, 2. 1908) has described a new Asplenium from Arizona.—C. B. ROBINSON (Bull. Torr. Bot. Club **35**:63–75. 1908) has begun a series of contributions bearing the title "Alabastra philippinensis," the first one containing descriptions of 12 new species.—P. C. STANDLEY (*idem* 77–78) discusses certain New Mexican forms of Echinocereus and describes a new species.—H. D. HOUSE (*idem* 89–90) has described 2 new species of Evolvulus from the Bahama Islands.—E. GILG (Bot. Jahrb. **40**:444–518. 1908), in an account of the African Flacourtiaceae, describes numerous new species and the following new genera: *Trichostephanus*, *Marquesia*, and *Ophiobotrys*.—A. ENGLER (*idem* 519–572), among numerous new species of African plants, describes species under Gnetum, Loranthus (30), Viscum (7), and Garcinia (22), and a new genus (*Acanthotreculia*) of Moraceae.—B. L. ROBINSON (Rhodora **10**:29–35. 1908) has revised the nomenclature of a number of plants of the northeastern United States, chiefly of minor varieties and forms, and includes the description of a new Woodsia from Minnesota and Michigan.—G. HIERONYMUS (Hedwigia **47**:204–224. *pls. 1–4*. 1908), in an account of the pteridophytes of STÜBEL'S South American collections, describes new species under Diplazium (8) and Asplenium.—R. KELLER (Bull. Herb. Boiss. II. **8**:175–191. 1908), in a revision of Hypericum § Brathys, recognizes 21 species, 6 of which (from South America and Mexico) are described as new.—L. L. CAPITAINE (*idem* 251–253) has described a new genus (*Hyalocalyx*) of Turneraceae from Madagascar.—

M. L. FERNALD (Rhodora **10**:46–55. 1908), in notes on some plants of northeastern America, publishes a number of new combinations, forms, and varieties, and also new species under Potamogeton, Fragaria, Callitriche, and Vaccinium.—A. FINET (Bull. Soc. Bot. France IV. **7**:531–538. 1908) has published a new genus (*Pseudoliparis*) of Orchidaceae from China, and also (*idem*, Mémoires, pp. 65. *pls. 12*) an account of African orchids of the tribe Sarcantheae, including many new species and the new genera *Monixus*, *Rhaphidorhynchus*, *Ancistrorhynchus*, and *Dicranotaenia*.—F. GAGNEPAIN (*idem* 538–544) has described two new genera (*Oligolobos* and *Xystrolobos*) of Hydrocharitaceae from China.—T. MAKINO (Bot. Mag. Tokyo **22**:14–20. 1908) has described the new genera *Alectorurus* (Liliaceae) and *Tubocapsicum* (Solanaceae) from Japan.—S. OKAMURA (*idem* 29–31, 41–44. *pls. 2, 3*) has published two new genera (*Orthomniopsis* and *Okamuraea* Broth.) of mosses from Japan.—MARCUS E. JONES (Contrib. Western Bot. No. 12. pp. 100. 1908) has described numerous (96) new species of western plants, including *Scopulophila* (Illecebraceae) and *Cusickia* (Umbelliferae) as new genera; and has critically reviewed the western Umbelliferae, adopting Cogswellia to replace Peucedanum.—W. R. MAXON (Contrib. U. S. Herb. **10**:473–503. *pls. 55, 56*. 1908), in the first number of a series of studies of tropical American ferns, has described as new genera *Holodictyum* (an "asplenioid fern") and *Ananthacorus* (allied to Vittaria), and several new species.—J. M. GREENMAN (Field Columb. Mus. Publ. Bot. **2**:247–287. 1908), in a paper on new or noteworthy spermatophytes from Mexico, Central America, and the West Indies, has described new species under numerous genera, 25 species of Senecio being new or fully characterized for the first time, and *Goldmania* (Coreopsideae) being a new genus.—D. PRAIN (Kew Bull. **1908**:114) has described a new genus (*Acrymia*) of Labiatae from Malaya.—J. M. C.

Diseases of apples.—BURRILL[2] and BLAIR[3] have published two bulletins presenting what may be considered a summary of their extensive investigations of the bitter rot of apples, both as to its botanical relations and methods of control and eradication by removal of the cankers and proper spraying methods. Few orchard diseases have received such attention, and every orchardist and plant pathologist should read these two publications, which are too extensive to be summarized here.

STEVENS and HALL[4] have recently published a description of several apple diseases. The volutella rot of the fruit is due to *Volutella fructi* Stevens and Hall. *Coniothyrium fuckelii* Sacc. is recorded as causing a fruit rot and also producing

[2] BURRILL, T. J., Bitter rot of apples. Botanical investigations. Bull. Ill. Exp. Stat. **118**:553–608. *pls. 10*. 1907.

[3] BLAIR, J. C., Bitter rot of apples. Horticultural investigations. Bull. Ill. Exp. Stat. **117**:481–552. *pls. 2*. 1907.

[4] STEVENS, F. L., and HALL, J. G., Some apple diseases. Bull. N. Car. Exp. Stat. **196**:37–55. *figs. 5*. 1907.

cankers on the twigs. Twig cankers due to the black rot fungus (Sphaeropsis) is also reported as being frequent. Apple scurf, a twig disease, is described as due to Phyllosticta or *Phoma prunicola*.—E. MEAD WILCOX.

The roots of Lycopodium Selago.—Miss SAXELBY[5] has studied the origin of the roots of *Lycopodium Selago*, working with young plants grown from bulbils. She reports that the roots arise near the apex of the stem, but below the first leaves, and grow down through the cortex of the stem, emerging at the level of the ground. It is probable that "origin below the first leaves" is too sweeping a statement, for in preparations made by the reviewer from the same species the roots usually arise higher up than the first leaf. Miss SAXELBY finds that the dermatogen of the root arises from several cells of the innermost layer of the stem periblem; while the periblem and plerome arise from the plerome of the stem. It is interesting to note that the author finds three meristematic regions: plerome, periblem, and a dermatogen which forms both epidermis and root cap. The roots are usually diarch, with the metaxylem in the form of a horseshoe; but they may be tetrarch, with the metaxylem in two parallel bands; or there may be a transition between the two conditions.—ALMA G. STOKEY.

Germination of Fucus.—KNIEP finds ninety pages barely sufficient to relate and discuss the observations of three and a half months, at Bergen, on the physiology of fertilization and germination in *Fucus serratus*, *F. vesiculosus*, and *F. spiralis*.[6] After a serious attempt it appears impracticable for the reviewer to discover in this voluminous paper the author's results and conclusions, for he does not make clear the outcome of his work, nor anywhere give so much as a line by way of summary regarding a single topic. His observations were directed particularly to the influence of external factors on the gametes and sporelings. The main topics are the effect of concentration of the total salts in sea water upon the movement of sperms, fertilization, germination, and geographical distribution; the influence of temperature (brief); the directive and formative effects of light; certain phases of regeneration in sporelings; and finally the possible induction of polarity by chemical stimuli.—C. R. B.

Californian Hepaticae.—HUMPHREY publishes together a series of notes on the physiology and morphology of certain Californian Hepaticae.[7] He reports that *Fossombronia longiseta*, *Fimbriaria californica*, *Aneura multifida*, *Anthoceros Pearsoni*, and *Porella Bolanderi* are infested commonly with fungi, parasitic in the first case, symbiotic in the second, and epiphytic in the last three. In *Fegatella conica* fertilization occurs in early spring, the spores pass the dry

[5] SAXELBY, E. MARY, The origin of the roots in *Lycopodium Selago*. Annals of Botany **22**:21–33. *pl. 3*. 1908.

[6] KNIEP, H., Beiträge zur Keimungs-Physiologie und -Biologie von Fucus. Jahrb. Wiss. Bot. **44**:635–724. *figs. 12*. 1907.

[7] HUMPHREY, H. B., Studies in the physiology and morphology of some California Hepaticae. Proc. Wash. Acad. Sci. **10**:1–50. *pls. 1, 2*. 1908.

season in the tetrad stage, and mature early in January. Various adaptations to a dry season are noted. Hygrophilous species are unable to recover from desiccation, but both thallus and spores of xerophilous ones grow promptly even after complete artificial desiccation. The remaining studies are concerned with the germination of spores of various species, and the brief life of the green or thin-walled spores, as contrasted with those of certain xerophilous species which are known to be viable after two years.—C. R. B.

Florida strangling figs.—BESSEY[8] has studied the germination and habits of the two native figs of Florida (*F. aurea* and *F. populnea*). In dense hammocks *F. aurea* begins only as an epiphyte, but eventually all trace of this habit is lost; while in open places it is often independent from the first. This seems to be explained by the fact that the seeds germinate only in the light, and experiments were performed to prove this peculiar habit. Following germination, the usual gradual "strangling" of the host plant occurs. Roots are sent down along the host plant and established in the ground, and finally by anastomosing and growth they completely incase the host. Both species have two or more crops of fruit each year, and are pollinated by different species of Blastophaga. Both kinds of flowers occur in the same receptacle, and the differentiation of the flowers is not so extreme as in the commercial fig.—J. M. C.

Morphology of Asimina triloba.—HERMS[9] has discovered the following facts in a study of *Asimina triloba:* the ovule passes the winter in a stage preceding the differentiation of the archesporial cell; the megaspore tetrad is occasionally tetrahedral instead of linear; the embryo sac becomes remarkably elongated; the polar nuclei remain in contact for three weeks or more; the antipodals are very ephemeral; the first segmentation of the egg does not occur for three or four weeks after fertilization; the first division of the endosperm nucleus is accompanied by transverse wall formation, dividing the linear sac into two equal chambers, the transverse divisions continuing until the sac contains a linear series of about twelve cells, when longitudinal division begins at the antipodal end; the embryo is very small and little organized even in the seed.—J. M. C.

Light and germination of fern spores.—LIFE[10] has been experimenting with the effect of light of different intensities upon the germination of fern spores. The spores of *Alsophila australis* germinated about a year after collection, but the spores of other ferns germinated as soon as they were dry. Under ordinary conditions the spores do not germinate in darkness; and at higher temperature

[8] BESSEY, ERNST A., The Florida strangling figs. Rept. Mo. Bot. Garden **1908**: 25:33. *pls. 1–9.*

[9] HERMS, WILLIAM B., Contribution to the life history of *Asimina triloba.* Ohio Naturalist **8**:211–217. *pls. 15, 16.* 1907.

[10] LIFE, A. C., Effect of light upon the germination of spores and the gametophyte of ferns. Ann. Rep. Mo. Bot. Gardens **19**:109–122. 1907.

than ordinary room temperature the spores of Alsophila and Aneimia could not be induced to germinate in darkness. Germination was best in light of medium intensity (about 0.075 sunlight). Weaker light induced filamentous or ribbon-like prothallia, while strong light induced heart-shaped prothallia. Strong light (intensity 0.3) cause the production of only archegonia in Alsophila, while in the other ferns both sex organs were produced. Weak light inhibits the production of archegonia and favors the production of antheridia.—J. M. C.

Poisonous action of salts.—BENECKE[11] mingles with a strong polemic against LOEW an account of experiments which go to show that various salts collectively harmless are individually poisonous to Spirogyra, but have their toxic action neutralized by calcium salts. The chlorids, nitrates, sulfates, and phosphates of sodium, potassium, magnesium, and iron are more or less poisonous. The cations Fe and Mg are more poisonous than K, itself more poisonous than Na; of the anions named the phosphate, sulfate, and nitrate are more poisonous than chlorion. The toxicity of both anions and cations may be removed or diminished by the addition of Ca ions.

These results are essentially those obtained by OSTERHOUT and DUGGAR, the chief difference being that BENECKE ascribes to Ca a special antitoxic property toward other salts.—C. R. B.

Respiration and pollination.—When the gynaecium begins its second phase of development, after pollination, the respiratory activity might be expected to differ from that of an unpollinated one, but no comparative determinations seem to have been made. This has now been done by Miss JEAN WHITE,[12] using the Bonnier-Mangin apparatus for gas analysis. With due precautions she finds this apparatus, as modified by AUBERT, entirely satisfactory. "The net result of the whole work is to show that pollination not only produces a rapid rise of the respiratory activity, but also affects the respiratory quotient," which is usually less than unity and larger in the pollinated than in the unpollinated gynaecium. The numerical data show such extraordinary differences, under presumably like conditions, as to raise serious question regarding the value of the observations. —C. R. B.

Embryology of Oxalis.—HAMMOND[13] has investigated *O. corniculata* and records that the single hypodermal archesporial cell does not give rise to any parietal tissue, but functions directly as the megaspore mother cell, which he calls the megaspore; that the antipodals disappear soon after fertilization; and that the basal cells of the suspensor form a very active haustorium.—J. M. C.

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[11] BENECKE, W., Ueber die Giftwirkung verschiedener Salze auf Spirogyra, und ihre Entgiftung durch Calciumsalze. Ber. Deutsch. Bot. Gesells. **25**:322–337. 1907.

[12] WHITE, JEAN, The influence of pollination on the respiratory activity of the gynaecium. Annals of Botany **21**:487–499. 1907.

[13] HAMMOND, HOWARD S., The embryology of *Oxalis corniculata*. Ohio Nat. **8**:261–264. *pl. 18*. 1908.

NEWS

DR. H. O. JUEL, formerly assistant professor, becomes professor of botany in the University of Upsala.

MR. L. L. BURLINGAME, The University of Chicago, has been appointed instructor in botany in Stanford University.

MISS ALMA G. STOKEY, The University of Chicago, has been appointed instructor in botany in Mount Holyoke College.

DR. CARLTON C. CURTIS, Columbia University, has been advanced from an instructorship in botany to an adjunct professorship.

MISS E. N. THOMAS, University College, London, has been appointed head of the department of botany in Bedford College for Women.

DR. LAETITIA M. SNOW (Chicago), State Normal School, Farmville, Virginia, has been appointed instructor in botany in Wellesley College.

DR. F. D. HEALD, University of Nebraska, has been elected to a professorship in botany in the University of Texas, to succeed Dr. W. L. BRAY, who has gone to Syracuse University.

MR. H. MIGLIORATO has undertaken to prepare a systematic dictionary of plant pathology, and asks botanists to send their papers to him at the Botanical Institute, via Panisperna 89B, Rome.

CARL WARNSTORF (Berlin-Friedenau) announces for sale his large collection of Sphagnum, containing about 30,000 specimens from all parts of the world, and also a very large number of annotations and memoranda.

THE TWENTY-FIFTH YEAR of the professorship of Dr. KARL GOEBEL at the University of Munich was celebrated on March 7. More than fifty botanists were present, and Professor GOEBEL received a number of valuable presents from his former students, and greetings from many universities.

THE COMMITTEE in charge of securing a botanical foundation in honor of LEO ERRERA announces that the necessary amount has been subscribed. The income will be used for the encouragement of research, and information may be obtained from Professor J. MASSART, rue Albert de Latour 44, Brussels.

HERBERT F. ROBERTS, Kansas State Agricultural College, has received a commission from the Kansas Experiment Station to inspect the wheat regions of Southern and Central Europe during the coming summer. He will visit Italy, Greece, the Balkan states, and Hungary, and also the notable plant-breeding stations.

DR. OŞKAR BREFELD, having been compelled by serious trouble with his eyes to give up the editorship of *Cohn's Beiträge zur Biologie der Pflanzen*, the duty has been assumed by Professor FELIX ROSEN of the University of Breslau. The second and concluding part of the ninth volume has recently appeared after an interval of several years.

THE LARGE and valuable herbarium of the late Mr. A. P. MORGAN has been presented to the State University of Iowa by his widow. It includes his botanical library, and is undoubtedly the most complete collection in existence of the mycologic flora of the lower valley of the Ohio River, and must always remain of importance on account of the numerous types it contains.

THEODOR OSWALD WEIGEL (Leipzig) has issued the first number of a paper entitled *Herbarium*, which will be published bimonthly, and is to be devoted to the distribution of *exsiccata*. It will announce continuations of current collections, collections that are wanted, and those that are offered. The publisher feels that this handling of dried plants in addition to botanical books will prove of advantage to many botanists and botanical establishments.

The following summer laboratories, in addition to those already noticed, announce botanical instruction and research: Marine Biological Laboratory, Woods Hole, Mass., July 1 to August 11 (GEORGE F. MOORE, JOHN M. COULTER, GEORGE R. LYMAN, C. J. CHAMBERLAIN, R. R. GATES, C. H. SHATTUCK, W. R. MAXON); Biological Laboratory, Cold Spring Harbor, L. I., July 1 to August 11 (D. S. JOHNSON, GEORGE D. FULLER, HARLAN H. YORK); Lake Laboratory, Cedar Point, Ohio, June 22 to July 31 (MALCOM E. STICKNEY); Harpswell Laboratory, South Harpswell, Maine, June 15 to September 15, purely research.

THE EDITORS OF THE BOTANICAL GAZETTE have decided to discontinue the **Items of taxonomic interest,** heretofore a feature of "Notes for Students." Their chief purpose was to serve taxonomists in calling attention to new genera and to new American species. There was not space enough to do this completely, and anything short of completeness in such a record is unsatisfactory. Besides, this useful service is now more fully rendered by the *Botanisches Centralblatt* and FEDDE'S *Repertorium novarum specierum*, to say nothing of the various current card indexes. This does not mean that taxonomic literature will be neglected, but that it will be reviewed selectively, as in the case of other literature.

WITH THE PRESENT NUMBER of the BOTANICAL GAZETTE, the department of "NEWS" will be discontinued. Botanical news is now more promptly announced for American readers in *Science* than it can be in a monthly journal; and foreign readers receive such information through journals nearer at hand.

GENERAL INDEX

The most important classified entries will be found under Contributors, Personals, and Reviews. New names and names of new genera, species, and varieties are printed in **bold-face** type; synonyms in *italic*.

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